Science to inform habitat restoration for woodland bird communities of the Tasmanian Midlands

Glen C. Bain

BSc., MSc. The University of Melbourne.

UNIVERSITY *of* TASMANIA

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School of Natural Sciences, University of Tasmania

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“Dame Nature has built up a perfect machine of bird-life, but man has upset the synchronization by eliminating certain parts of the machine and introducing others. With the more advanced knowledge we have at the present day it behoves us to take more care of Nature's machinery, and if this is done I feel sure we can all look forward with confidence to the future of ornithology in Tasmania.”

– Clive Errol Lord 1933

Director of the Tasmanian Museum and Art Gallery,

President of the Royal Australasian Ornithologists' Union

Declaration of originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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Permits and licensing

This project was undertaken with approval from the University of Tasmania Animal Ethics Committee (permit A14880) and Department of Primary Industries, Parks, Water and the Environment (permits TFA15132, TFA16138, TFA17103).

Statement of contribution & co-authorship

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

Candidate: Glen Bain, School of Natural Sciences, University of Tasmania (UTAS), Hobart, Tasmania, Australia (GB)

Author 1: Menna Jones, School of Natural Sciences, University of Tasmania (UTAS), Hobart, Tasmania, Australia (MJ)

Author 2: Chris Johnson, School of Natural Sciences, University of Tasmania (UTAS), Hobart, Tasmania, Australia (CJ)

Author 3: Michael MacDonald, Centre for Conservation Science, Royal Society for the Protection of Birds, Bedfordshire, United Kingdom (MM)

Author 4: Riana Gardiner, School of Natural Sciences, University of Tasmania (UTAS), Hobart, Tasmania, Australia (RG)

Author 5: Rowena Hamer, School of Natural Sciences, University of Tasmania (UTAS), Hobart, Tasmania, Australia (RH)

Chapter Three has been submitted to the journal *Open Science* and is under review. All authors conceived and planned the manuscript; MM collected the historical bird data; GB, RG and RH collected the vegetation data; GB collected the contemporary bird data, completed the analysis and wrote the manuscript, with feedback and review from all authors.

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We the undersigned agree with the above stated proportions of work undertaken for each of the above published (or submitted) peer-reviewed manuscripts contributing to the thesis:

_____ _____

Assoc. Prof. Menna Jones
Primary Supervisor
School of Natural Sciences
University of Tasmania
Dated: 27th May 2019

Prof. Chris Johnson
Supervisor
School of Natural Sciences
University of Tasmania
Dated: 27th May 2019

_____

Assoc. Prof. Greg Jordan
Head of Discipline
Discipline of Biological Sciences
School of Natural Sciences
University of Tasmania
Dated: 27th May 2019

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Abstract

Agricultural intensification over the last 50 years has been a major cause of global biodiversity decline and continues to result in habitat loss, fragmentation and degradation. The agriculture sector must increase production to feed a rapidly growing human population but, to be sustainable, must also maintain the ecosystem services provided by the biodiversity on which it relies. Just how to achieve this is the current focus of much scientific debate. What is clear, is that the world's current estate of protected areas is no longer sufficient to conserve healthy wildlife populations. Ecological restoration of degraded farmland and patches of remnant habitat will be necessary if we are to halt, and ultimately reverse, trends of biodiversity loss.

Populations of many birds are declining in agricultural landscapes around the world. Agricultural intensification has been suggested as the primary cause of these declines through processes such as increased pesticide use, mechanisation of farming practices and the removal of critical habitat features including hedgerows, large old trees, wetlands and coarse woody debris. The impacts of land use intensification on avifauna have been best studied in the "farmland birds" of Europe and North America, but in Australia it is "woodland birds" that are of most conservation concern. Woodland birds are increasingly threatened because of their restriction to ever smaller patches of remnant habitat surrounded by agriculture, where they are vulnerable to edge effects, exotic predators and higher levels of interspecific competition.

A primary goal of the thesis is to describe current patterns of patch occupancy and abundance of birds in the agricultural Midlands region of Tasmania, Australia, and explore the processes that underlie those patterns. Despite having high biodiversity value, very little

is known about the current state of terrestrial avifauna in Tasmania, especially in the Midlands. The data collected in this thesis will be used to guide local landscape restoration efforts and inform decisions on which habitat features are most important to restore for Tasmanian birds, what species could be selected as targets for restoration, and how birds might respond to future environmental change, whether that be continued habitat loss or revegetation.

In the first data chapter, I surveyed birds at 72 sites across the Midlands including in woodlands that had previously been surveyed 20 years ago. I used new statistical techniques to determine which elements of habitat are most important in influencing the composition of woodland bird communities and compared contemporary survey data with historical records to understand how birds have responded to land use change over the last two decades. The amount of woodland cover at survey sites, structural complexity of vegetation and the presence of an aggressive honeyeater species, the noisy miner (Man*orina melanocephala*), had the strongest effects on birds. Small to medium-sized arboreal foragers appear to have declined while large-bodied granivorous birds have increased. I make practical recommendations for the restoration of habitat for local avifauna, paying particular attention to the threat that noisy miners pose to ongoing restoration efforts.

In the second data chapter, I seek a deeper understanding of how noisy miners might exclude other bird species from suitable woodland habitat. Noisy miners are well recognised in Australia as a leading cause of population decline in small woodland birds. Indeed, in Chapter Three, changes in the abundance of noisy miners was identified as a key factor in explaining changes in species richness at survey sites and their presence had a

strong influence on patch occupancy by small birds. Noisy miners have benefitted from agricultural habitat loss and fragmentation and now dominate remnant woodlands throughout the eastern states. I tested the hypothesis that interference competition with miners could result in chronic stress among cohabiting bird species, with the potential to force individuals to abandon miner-dominated habitat or otherwise reduce fitness such that they can no longer persist. I captured 86 individuals of a model passerine species, the superb fairy-wren (*Malurus cyaneus*) from six woodland sites, three with miners and three without, and used heterophil-to-lymphocyte (H:L) ratios to infer relative levels of chronic stress. H:L ratios were 1.8 times higher in fairy-wrens from remnant woodlands occupied by miners, suggesting higher levels of physiological stress. H:L ratios were also negatively associated with the residual mass of fairy-wrens and positively associated with the presence of a blood parasite, *Haemoproteus* spp. Noisy miner presence might also be correlated with other potential stressors, such as food scarcity, in small patches of degraded habitat. I suggest further experiments to clarify whether conflict with miners is the proximate cause of chronic stress in fairy-wrens living in remnant woodlands.

Finally, I applied new techniques to test a long-hypothesised mechanism for bird declines in agricultural landscapes: a high frequency of nest predation due to changes in habitat structure or an increased abundance of nest predators. I used motion-sensor cameras to monitor 84 nests of brown thornbills (*Acanthiza pusilla*) and superb fairy-wrens, and terrestrial LiDAR to quantify the three-dimensional structure of vegetation at nesting sites. A diverse range of predators were recorded preying on nests, but overall rates of predation were no higher than previously recorded for these species living in non-agricultural landscapes. Daily survival rates (DSR) of nests were influenced by the amount of nearby edge habitat, nest height, surrounding woodland cover and the density of

vegetation, although the direction of these effects was not always as predicted. DSR declined with increasing vegetation clutter at nest sites and was higher in areas with more edge habitat. I suggest that nest predation in fairy-wrens and thornbills is higher in larger and more intact woodlands because this habitat supports a greater abundance of native predators.

My results indicate that restoration practitioners working in the Midlands should focus on restoring structural complexity of vegetation in remnant habitat, particularly in the midstorey, to provide small and medium-sized birds with protection from noisy miners, safe nesting sites and suitable foraging habitat. Connecting remnant woodlands through planting wildlife corridors will benefit some birds simply through increasing levels of wooded cover but this should be done with caution to mitigate the risk of noisy miners further increasing their distribution. I strongly encourage a continued long-term monitoring effort in restored areas as they mature to ensure that restoration sites do not constitute an ecological trap, whereby birds prefer these habitats but their fitness is reduced. While any form of bird data collected in the Tasmanian Midlands will prove useful, it is important that future monitoring moves beyond measuring the occurrence of species and extends to the survival, growth and reproductive success of individual birds.

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Chapter One

General Introduction

Birds of the Tasmanian Midlands.

The value of farmland biodiversity and costs of agricultural intensification

The human population is expected to reach 9.8 billion by 2050 and is becoming increasingly wealthy (United Nations 2017). This is projected to increase global food demand by between 25-70% (Hunter *et al.* 2017a). To meet this demand the agriculture sector must increase production but at the same time address the environmental challenges posed by climate change, global biodiversity loss and a prevailing decline in ecosystem function. In the past, farms have increased productivity through the conversion of natural habitats to cultivated land. Approximately 40% of the Earth's land surface is now used for agriculture, 1.6 billion hectares (12%) of which is used for crop production (Foley *et al.* 2005; Alexandratos & Bruinsma 2012). More recently, however, farms have been able to improve yields without further expansion through a number of processes that have been collectively termed *Agricultural Intensification*.

The processes involved in agricultural intensification include the mechanisation of farming practices, rising levels of chemical use (fertilisers, antifungals, herbicides and insecticides), increased use of irrigation and tillage, changing crop rotations, the expansion of monocultures and the consolidation of smallholder farms into larger industrialised ones (Chamberlain *et al.* 2000; Emmerson *et al.* 2016; Stanton *et al.* 2018). Agricultural intensification results in the broad simplification of landscapes through clearing of small patches of remnant vegetation and the removal of natural features such as wetlands, rocky outcrops and scattered paddock trees (Hunter *et al.* 2017b).

These changes to agricultural landscapes come at the expense of native wildlife populations. While singularly focussed on improving food security or economic gains, modern agriculture has failed to acknowledge its reliance on the services provided by

functional ecosystems, including those that native flora and fauna provide. For example, invertebrate populations are vital for crop pollination and the maintenance of soil fertility on farms (Prather *et al.* 2013), and birds have been shown to control insect pests and improve yields in a variety of agricultural systems, including in crops of apples (Peisley *et al.* 2016), alfalfa (Kross *et al.* 2016) and wine grapes (Jedlicka *et al.* 2011).

Farmland bird declines in Europe & North America

Birds are one faunal group well documented to have declined severely under agricultural intensification. In Europe, "farmland birds" have experienced continent-wide declines (Chamberlain *et al.* 2000; Donald *et al.* 2006; Wretenberg *et al.* 2010) and common species are declining at faster rates than less common birds (Inger *et al.* 2015). Two mechanisms of population decline are of particular concern across Europe: loss of nesting and foraging habitat due to clearing of hedgerows; and broad-scale application of pesticides on farms (Boatman *et al.* 2004; Hinsley & Bellamy 2019).

Various styles of hedgerow have traditionally been used to delineate field boundaries and hold livestock throughout the European countryside (Dover 2019). Hedgerows are an important source of food, refuge and nesting sites for farmland birds and can facilitate their dispersal through the agricultural matrix (Lecq *et al.* 2017; Hinsley & Bellamy 2019). More intensive farming of cereals has imposed larger field sizes, resulting in wholesale destruction of hedgerows. An estimated 41% of Britain's managed hedgerows have been lost since the late 1950s and over 1 million kilometres of hedges were cleared in France over a period of just 50 years (Pointereau *et al.* 2001; Dover 2019).

In April 2018, the European Union (EU) banned outdoor use of the world's most commonly applied pesticide group, neonicotinoids. The ban came primarily because of the

risk posed by neonicotinoids to wild honeybee populations (Pisa *et al.* 2015) but their use may have also contributed to declines in farmland birds. Neonicotinoids can be lethal to birds that feed on treated plants and grain, and have devastating sublethal effects on the reproductive output, flying ability and immune function of birds (Wood & Goulson 2017). Further, neonicotinoids and other classes of insecticide may have had indirect trophic effects on farmland birds through reductions in insect prey. Hallmann *et al.* (2014) revealed that population trends of species in the Netherlands were more negative in areas where neonicotinoid concentrations were highest and that bird declines began with the first use of these chemicals. Neonicotinoids remain widely used in Australia, the United States and China but have been partially banned in Canada and are currently under review in New Zealand (Umina *et al.* 2018; Chen *et al.* 2019). Concerns remain in the EU over the use of alternative pesticides and the threats that they too might pose to birdlife.

Alarming patterns of farmland bird decline have also been recorded in North America. Stanton *et al.* (2018) considered 77 North American species and found that 57 (74%) had experienced population decline between 1996 and 2013. Aerial insectivores (mean decline of -39.5%) and grassland birds (-20.8%) have been most affected by agriculture. The latter are decreasing at rates of nearly 4% annually in some productive landscapes of the United States (West *et al.* 2016). Stanton *et al.* (2018) suggested that two likely mechanisms causing these declines are the widespread conversion of native grassland prairies, and as suggested for bird declines in Europe, a collapse in insect prey populations owing to pesticide use.

While the effects of agricultural intensification on farmland birds are overwhelmingly negative, some species have benefitted from changes in land use. The largest beneficiaries

in the Northern Hemisphere appear to have been corvids, which have exploited the additional food resources that farms provide (livestock carcasses, spilt grain & better access to soil invertebrates, Gregory & Marchant 1995; Fuller & Gough 1999; Gade 2010; Stanton *et al.* 2018). The same might be true for corvids in Australian farm landscapes (Chapter Three). Certainly, mobile species with generalist diets from a range of taxa have coped better with agricultural intensification than habitat specialists (Wickramasinghe *et al.* 2003; Ekroos *et al.* 2010; Fried *et al.* 2010). Ravens (*Corvus* spp.) have increased in both North America and Europe (Roos *et al.* 2018) so much so that predation by ravens on other songbirds and their eggs has itself been proposed as a mechanism of avian population decline (Andren 1992; Madden *et al.* 2014).

Some farmland birds that have undergone dramatic declines in their native range have become significant invasive species in agricultural landscapes elsewhere. For example, numbers of common starlings (*Sturnus vulgaris*), a grassland invertebrate feeder, have reduced by more than 70% in Britain (Eaton *et al.* 2015) and are currently experiencing annual declines of over 2% in Denmark because of land use intensification (Heldbjerg *et al.* 2016). This has placed starlings among those species of highest conservation concern in the EU. Nonetheless, starlings have successfully spread and are increasing in agricultural regions of South America, New Zealand and Australia where they have been introduced (Roberts 2006; Macleod & Till 2010; Zufiaurre *et al.* 2016).

Woodland bird declines in Australia

Notwithstanding trends of population decline, farmland birds of the Northern Hemisphere are typically well adapted to living in agricultural landscapes. Farms in eastern Europe, for example, are so ancient that avifauna are thought to have coevolved with

agriculture such that many extant species prefer more open habitat types (Sutherland 2004). In more recently developed countries including Australia, birds that do well in farmland are a comparatively small subset of native species and a large suite of introduced species (Haslem & Bennett 2008). Consequently, it is woodland birds and forest dependent species that have attracted most conservation concern in Australia (Haslem & Bennett 2008).

There has been discussion over what exactly constitutes a "woodland bird" (Fraser *et al.* 2015) but below I use the term in its most general sense: birds that occur in woodlands and use this habitat for either foraging or nesting. Woodland birds are different from farmland birds in that most are not dependant on crops, pastures or semi-natural features like hedgerows for breeding or foraging (Attwood *et al.* 2009). They are, therefore, assumed to be more robust to changes in the agricultural matrix (e.g. crop rotations) and are unlikely to experience direct mortality from farm practices such as mowing. Indeed, Attwood *et al.* (2009) noted that processes occurring within the agricultural matrix have generally been neglected in Australia, perhaps because it is assumed that such processes have less influence on birds whose primary habitat is woodland. The largely ignored potential for pesticide use effects on Australian birds is a case in point (but see Kitulagodage 2011). Nonetheless, woodland birds in Australia are increasingly threatened by agricultural expansion and intensification and have recently been nominated for listing as a Threatened Ecological Community under the federal governments key environmental legislation, the *Environment Protection and Biodiversity Conservation* (EPBC) *Act*.

Woodland bird declines have been reported for several biogeographic regions in Australia, although the temporal coverage of population data is limited and more

quantitative studies of population trends are necessary (Rayner *et al.* 2014). As many as 28% of woodland bird species in the agricultural South-west Slopes region of New South Wales have experienced population decline in recent years (Lindenmayer *et al.* 2018). Nectarivores and ground-foraging insectivores appear to be of particular conservation concern and are disproportionately represented among declining species (Barrett *et al.* 2003; Lindenmayer *et al.* 2018). Worryingly, the latest iteration of the State of Australia's Birds also indicates that reporting rates for species long recognised as being common and widespread (for example the Australian magpie *Cracticus tibicen* and willie wagtail *Rhipidura leucophrys*) have reduced (BirdLife Australia 2015). Common species are thought to contribute most to ecosystem function and the delivery of ecosystem services (Winfree *et al.* 2015). Thus, the consequences of losing common birds could be disastrous.

Eighty to ninety percent of Australia's temperate eucalypt woodlands have already been cleared for urban and agricultural development (Lambert *et al.* 2000) and rates of deforestation are accelerating in some Australian states (Reside *et al.* 2017). There has been extensive secondary clearing of remnant habitat, riparian vegetation strips and keystone structures such as isolated paddock trees, owing to the expansion of irrigated lands and mechanised cropping (Attwood *et al.* 2009). Similar to the loss of hedgerows in Europe because of increasing field sizes (Dover 2019), the installation of large pivot irrigation systems throughout farm landscapes of Australia has necessitated larger paddock sizes and changes in paddock shape, leading to widespread clearing of shelterbelt vegetation – the nearest Australian equivalent to hedgerows. Habitat loss has been directly implicated in the decline of bird species, including for example the brown treecreeper (*Climacteris picumnus*), by disrupting their ability to disperse between woodland patches (Cooper & Walters 2002). Remaining woodland is largely restricted to poor-quality soils and remnant habitat is often

exposed to extremes of weather, for example, on hillsides not suitable for cultivation (Lindenmayer *et al.* 2010a; Watson 2011). Watson (2011) hypothesised that selective clearing of the most productive habitat could explain reduced numbers of insectivorous woodland birds because soils of lower fertility support fewer ground-dwelling invertebrates.

Habitat loss is undoubtedly the leading cause of woodland bird declines and historical land clearance might still contribute to current population trends through an extinction debt (Radford *et al.* 2005; Ford 2011). This is a phenomenon whereby an environmental disturbance such as land clearance might initially appear to be withstood by species but eventually results in their extinction without any further habitat modification (Kuussaari *et al.* 2009). This delayed response can lead to underestimates of numbers of threatened species and is a difficult concept for conservationists to identify and address (Kuussaari *et al.* 2009). Apart from habitat loss, various other underlying mechanisms have also been proposed as potential drivers of woodland bird decline (reviewed by Ford *et al.* 2001). These include: a decline in available nesting hollows (Manning *et al.* 2006; Koch *et al.* 2008); mortality caused by introduced predators like feral cats (*Felis catus*, Woinarski *et al.* 2017); increased competition with aggressive honeyeater species (Montague-Drake *et al.* 2011; Thomson *et al.* 2015); reduced quality and availability of food because of habitat degradation caused by overgrazing, the invasion of pastoral weeds and removal of coarse woody debris (Maron & Lill 2005; Razeng & Watson 2012); increased frequency of nest predation due to habitat degradation, higher abundance of mesopredators (e.g. ravens, currawongs *Strepera* spp., butcherbirds and magpies *Cracticus* spp., feral cats) or edge effects (Taylor & Ford 1998; Zanette & Jenkins 2000; Robertson *et al.* 2014); and climate change which has altered fire regimes and been linked to recent droughts (Mac Nally *et al.* 2009; Nimmo *et al.* 2015).

The weight of evidence supporting each of these mechanisms is varied (Ford 2011). One of the best studied and most certain processes to have affected woodland birds is a heightened level of interspecific competition with native honeyeaters of the genus *Manorina* (Thomson *et al.* 2015). This is a central theme in Chapters Three and Four of this thesis, but briefly, noisy miners (*M. melanocephala*) along with yellow-throated miners (*M. flavigula*) and bell miners (*M. melanophrys*) have benefitted from the degradation and fragmentation of remnant woodlands on farms, which has created habitats to which they are suited (Maron *et al.* 2013; O'Loughlin *et al.* 2017). Noisy miners especially, now dominate woodlands throughout eastern Australia and exclude smaller birds from what would otherwise be suitable habitat (Montague-Drake *et al.* 2011). A practicable solution to this major threat to woodland bird populations is yet to be identified despite decades of research on the subject (Grey *et al.* 1997; Piper & Catterall 2003; Davitt *et al.* 2018).

Given that nest predation is the main cause of reproductive failure in birds (Ricklefs 1969), surprisingly little attention has focussed on the potential for increased nest predation resulting from habitat change to cause woodland bird declines in Australia (Ford 2011). Habitat loss and deterioration can restrict breeding birds to small patches of remnant vegetation, resulting in higher nesting densities and predation rates (Keyser *et al.* 1998; Schmidt & Whelan 1999). Birds living in fragmented and degraded habitats might also be forced to select inferior nesting sites that are more vulnerable to predators (Major *et al.* 1999; Kentie *et al.* 2015) or mortality from agricultural practices (Pakanen *et al.* 2011). These interactions, together with increased abundance of many generalist and invasive nest predators on farms, (crows and racoon dogs *Nyctereutes procyonoides* in Europe [Roos *et al.* 2018; Krüger *et al.* 2018], racoons *Procyon lotor* and opossums *Didelphis virginiana* in North America [Dijak & Thompson 2000; Schmidt 2003], feral cats *Felis catus* and red foxes in

Australia [Doherty *et al.* 2017; Saunders *et al.* 2010]), are expected to result in higher rates of nest failure (Evans 2003). Remeš *et al.* (2012) found that rates of nest predation are indeed increasing among Australian songbirds but the cumulative impact this might have on bird populations is unknown.

Habitat change associated with agricultural intensification could have more subtle and indirect consequences for bird populations by elevating levels of physiological stress in individuals. The "stress response", which culminates in the release of glucocorticoid hormones (corticosterone in birds), is typically short-lived and adaptive (Romero & Wingfield 2016). Habitat loss, fragmentation and degradation, however, has the potential to cause *long-term* stress in wildlife (Hinam & Clair 2008; Johnstone *et al.* 2012). This may be via changes in the distribution and availability of key resources (e.g. reduced access to food or mates), modified predator-prey dynamics, increased levels of competition between and within species, disruptions to dispersal or increased exposure to human activities (Hinam & Clair 2008; Clinchy *et al.* 2013; Creel *et al.* 2013; George *et al.* 2014). Chronic stress has significant negative impacts on the reproduction, growth, immune function and survival of individuals (Ethan Pride 2005; Hing *et al.* 2016; Dudeck *et al.* 2018) that in theory could influence population demography, but the relevance of stress to woodland bird declines is not yet understood. Cosgrove *et al.* (2017) tested whether stress levels in eastern yellow robins (*Eopsaltria australis*) could be used to predict their probability of extinction from remnant woodlands in Queensland. Robins living in areas of low woodland cover have elevated levels of stress but there was no relationship between stress and localised extinctions (Maron *et al.* 2012; Cosgrove *et al.* 2017). Measurements of physiological stress have, nonetheless, provided early warning of population declines in other taxa and have

been suggested as a tool for obtaining a truer reflection of how animals perceive habitat quality than basic occupancy (Wikelski & Cooke 2006; Ellis *et al.* 2011).

Woodland bird declines are among the most pressing conservation issues in Australia. Understanding the processes causing these declines is, therefore, a major conservation priority and has attracted vast scientific inquiry. Despite this, the reasons for population declines of many species remain unclear (Watson *et al.* 2005; Watson 2011; Lindenmayer *et al.* 2018), partly because of inconsistencies in these trends between regions and habitat types (Barrett *et al.* 2003). Even without a complete knowledge of all the relevant processes, however, it is obvious that land clearing and degradation must cease in order to halt population decline. Moreover, countless authors have advocated for ecological restoration to play a central role in woodland bird conservation by increasing levels of woody vegetation cover, connecting remnant habitat and restoring structural complexity in degraded woodlands (Vesk & Mac Nally 2006; Taylor *et al.* 2008; Thomson *et al.* 2009; Lindenmayer *et al.* 2010b; Paton & O'Connor 2010; Huth & Possingham 2011; Smallbone *et al.* 2014; Ikin *et al.* 2018).

Restoring agricultural landscapes for wildlife

Scientists and land managers now acknowledge that for long-term viability, farms will need to better accommodate biodiversity. This has led to the emergence of agri-environment schemes and concepts such as sustainable intensification whereby agricultural output is enhanced while reducing its environmental impacts (Rockstrom *et al.* 2017; Nagothu 2018). Even so, it is widely recognised that ecological restoration will be necessary to reverse declines in farmland biodiversity. The United Nations has declared 2021-2030 to be the UN Decade on Ecosystem Restoration, defined as the process of assisting the

recovery of an ecosystem that has been degraded, damaged, or destroyed (McDonald *et al.* 2016). Ambitious restoration targets are already in place for large swathes of the world's degraded lands. For instance, the Bonn Challenge (founded in 2011) is a global initiative with the goal of restoring 350 million hectares of degraded forests and agricultural land by 2030. If achieved, the estimated benefit of the Bonn Challenge to the global economy is an enormous $U.S 2.25 trillion (Verdone & Seidl 2017).

Restoration ecology is a relatively young field of science with the journal of the same name turning 26 this year. To meet the global challenges in sustainable development that have been awarded to restoration ecology, the discipline's underlying scientific theory and practical application has rapidly advanced and must continue to do so. One concept in restoration ecology that is well-established, if patchily executed, is ecological monitoring (Rohr *et al.* 2018). Monitoring is essential to detect changes in the distribution and abundance of species, allows for early intervention by biodiversity managers and is necessary to determine if management interventions are effective. For monitoring to be useful, the International Standards for Ecological Restoration encourage monitoring of habitat condition and biodiversity at restoration sites both prior to and following restoration works, as well as monitoring reference sites in a comparable undisturbed ecosystem (McDonald *et al.* 2016).

Reference conditions are ideally represented by multiple locations where the structure, function, composition and diversity of native flora and fauna exist without having been altered by human disturbance (Reynoldson *et al.* 1997; Stoddard *et al.* 2006). For many regions, however, places of historical condition no longer occur and so reference conditions may alternatively apply to the best available habitat in an area otherwise

modified by human activity (Stoddard *et al.* 2006). Goals for restoration can be established using parameters measured at reference sites. This might include a list of target species, their densities, or some measure of the biotic processes that they fulfil (Rohr *et al.* 2018; Sinclair *et al.* 2018). Another important component of restoration programs is to establish a baseline of species presence and abundance prior to commencement, against which the success of restorative efforts can later be evaluated (i.e. control condition, Hale *et al.* 2019). Together, this information allows the trajectory of restoration to be assessed, whether its design should be adapted and can provide evidence to stakeholders that their investment is worthwhile (Sinclair *et al.* 2018).

Biodiversity responses to restoration have been poorly monitored. This is primarily due to a lack of funding for long-term research but also because enthusiasm for restoring degraded habitats has outpaced the basic science. Wildlife responses to restoration have been especially overlooked. At the 2017 international conference for the Society of Ecological Restoration, 96% of accepted abstracts focussed on plants or how animals could contribute to their dispersal (SER 2017). This is despite animals being increasingly acknowledged for their importance in the recovery of degraded land and ecosystem processes (Perring *et al.* 2015; McAlpine *et al.* 2016; Catterall 2018). Too often, restoration managers have adopted an "if we build it, they will come" approach towards wildlife (coined the *Field of Dreams Hypothesis*, Palmer *et al.* 1997) with the assumption that animals and ecological function will return to degraded areas once vegetation structure has been restored. Additionally, decisions on which features of vegetation should be restored have often drawn on human perceptions of habitat, rather than those of wildlife. The outcome is that many restoration plantings remain devoid of native animals or have only served as habitat for the most common species (Hale *et al.* 2017).

Jones and Davidson (2016) suggest an alternative approach to ecological restoration that focuses on the needs of animals and how they interact with the elements and configuration of the environment. They suggest using patterns of species abundance and occupancy along with behavioural information collected from individual animals to identify those elements of habitat that are most important to species, and accordingly, prioritise such features for restoration. This could increase the likelihood or speed with which animals colonise restored habitats, improve resilience in restored landscapes and help to maximise conservation outcomes.

The thesis explores the distribution and abundance of woodland birds in agricultural landscapes of the Tasmanian Midlands, where a large restoration program is underway, and some of the processes that might influence this. The restoration program (4 years and $6 million) is led by Greening Australia and the University of Tasmania, in collaboration with Bush Heritage Australia, the Tasmanian Land Conservancy, and the Tasmanian Department of Primary Industries, Parks, Water and Environment. A primary goal of the program is to connect extant woodlands to the east and west of the Tasmanian Midlands by two wildlife corridors, 10 000 hectares in extent, through plantings and the restoration of degraded remnant woodlands (Jones & Davidson 2016). My research contributes to an animal-centric approach to ecological restoration in the Midlands that uses behavioural information collected from individual animals to better inform practitioners on those habitat features that are most important to local wildlife (Fig. 1.1). My thesis is complemented by the works of four collaborating PhD researchers who studied habitat use and movement ecology of carnivores (spotted-tailed quolls *Dasyurus maculatus*, eastern quolls *Dasyurus viverrinus* and Tasmanian devil S*arcophilus harrisii*, Hamer 2019), microbats (suborder *Microchiroptera,* Dixon 2019 *unpublished data*), critical weight range mammals (eastern

bettongs *Bettongia gaimardi*, and eastern barred bandicoots *Perameles gunnii*, Gardiner 2018) and the landscape genetics of spotted tailed quolls and eastern bettongs (Proft 2018).

Aims & Thesis Structure

The thesis consists of three data chapters as well as this introduction, the following account of the study system and a final synthesis. Each data chapter is presented as a manuscript intended for publication, the aims of which are summarised below. Apart from addressing the specific research questions described in each chapter, the data collected here are being used to guide decisions by restoration practitioners working in the Tasmanian Midlands and have been shared with local landholders and school groups to build upon their personal connections with the wildlife of which, ultimately, they are the caretakers. My research will provide context to ongoing landscape restoration efforts such that their effectiveness at providing habitat for birds can be gauged in future.

Chapter 3

Long-term change in bird communities of an agricultural landscape: declines in arboreal foragers, increases in large species. In this chapter, I describe the current state of woodland bird communities in the Tasmanian Midlands and explore how changes in land use over the past 20 years might have influenced patch occupancy and abundance of bird species. I conducted bird and vegetation surveys across 72 sites in the Midlands and used multivariate statistical analyses (*manyGLM*) to test which environmental factors are most important in determining current patterns of bird community composition. I used historical data collected near the onset of agricultural intensification in the Midlands to assess changes in bird abundance and specifically tested for the effects of changes in woodland cover and noisy miner density on species richness at survey sites. Lastly, I tested whether functional

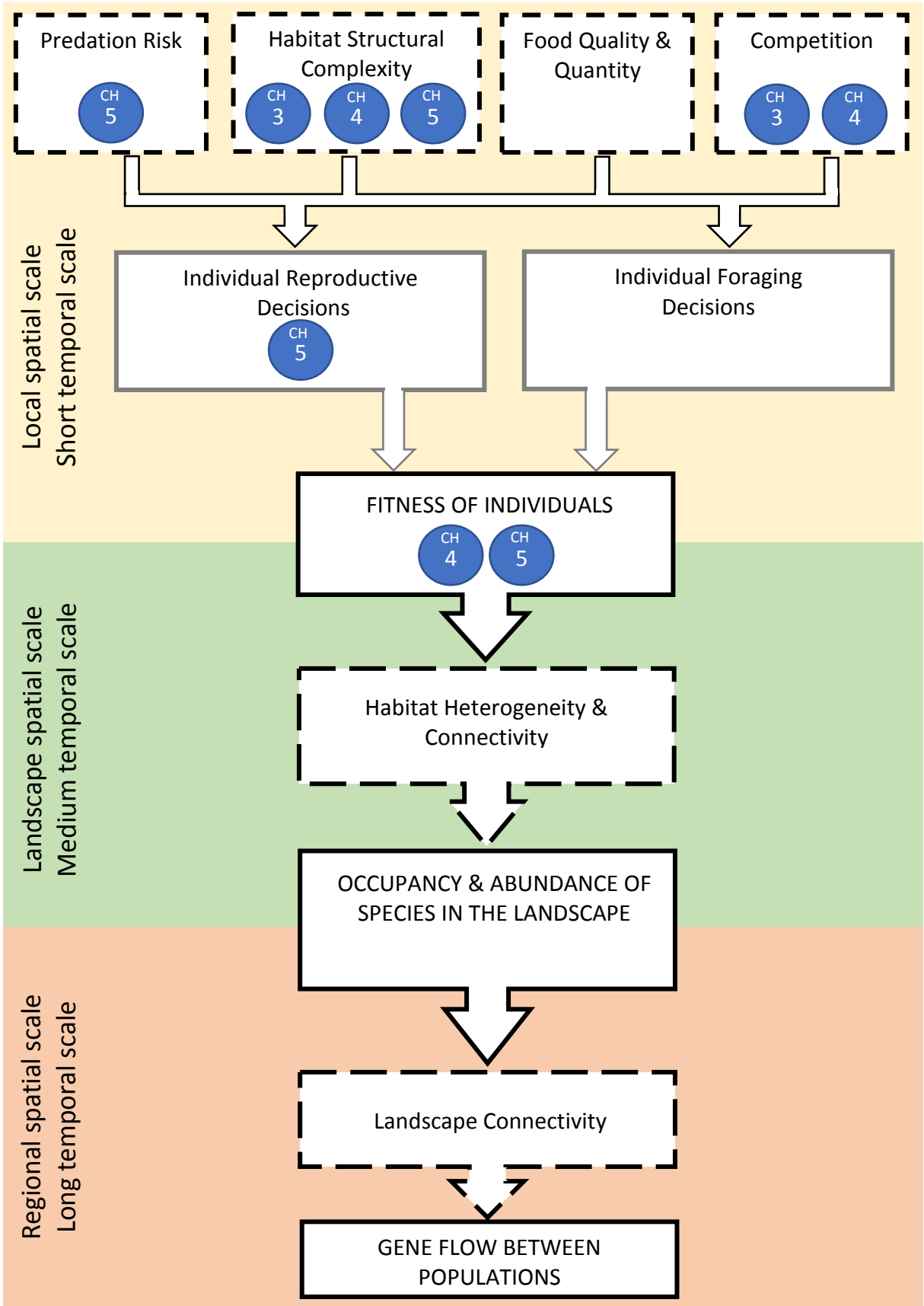
Predation Risk
CH 5
Habitat Structural Complexity
CH 3
CH 4
CH 5
Food Quality & Quantity
Competition
CH 3
CH 4
Local spatial scale
Short temporal scale
Individual Reproductive Decisions
CH 5
Individual Foraging Decisions
FITNESS OF INDIVIDUALS
CH 4
CH 5
Landscape spatial scale
Medium temporal scale
Habitat Heterogeneity & Connectivity
OCCUPANCY & ABUNDANCE OF SPECIES IN THE LANDSCAPE
Regional spatial scale
Long temporal scale
Landscape Connectivity
GENE FLOW BETWEEN POPULATIONS
Relevant Thesis Chapter
Potential restoration lever
Mediating process
OBSERVED PATTERN

Figure 1.1. Conceptual framework adapted from Jones and Davidson (2016). Individual foraging and reproductive decisions made by animals at local scales contribute to occupancy and abundance of species and the fitness of populations at larger scales. Models for ecological restoration have traditionally focused on improving habitat amount and connectivity without considering the behavioural decisions of individual animals, the factors driving those decisions and how these contribute to observed patterns of species abundance and occupancy in the landscape. Moreover, "habitat" has most often been defined by anthropocentric perceptions of vegetation rather than those of animals. An animal-centric approach to ecological restoration posits that by understanding fine-scale interactions between individual animals and their environment, practitioners will be better able to use these as levers for improving restoration outcomes.

traits of birds (e.g. body size, diet, migratory behaviour) explain their response to land use change. In doing this, I hoped to gain a better understanding of the mechanisms contributing to population trends of local species. The results of this chapter help to identify target species for ecological restoration in the Midlands and provide baseline data on bird community composition against which the success of restoration plantings can be gauged as they mature. Models of change in species richness and woodland cover that are included in this chapter will further our ability to predict bird species responses to local revegetation efforts.

Chapter 4

Chronic stress in superb fairy-wrens occupying remnant woodlands: are noisy miners to blame? The results of Chapter One and many earlier studies of woodland birds in Australia highlight the importance of a native honeyeater, the noisy miner (*Manorina melanocephala*), in controlling patterns of abundance, occupancy and population decline in other species. The exclusion of woodland birds from suitable habitat by aggressive noisy

miners is listed as a Key Threatening Process under Australian environmental legislation. It has been suggested that conflict with noisy miners might cause physiological stress in cohabiting species, reducing their ability to persist in miner-dominated habitat. In this chapter, I present an initial test of this hypothesis. I use differential white blood cell counts (heterophil-to-lymphocyte ratios) to compare stress levels between individuals of a small passerine, the superb fairy-wren (*Malurus cyaneus*), living in remnant woodlands on farms where miners were common and in more intact habitat without noisy miners. I also assess relationships between chronic stress levels in fairy-wrens, their body condition and infection by a cosmopolitan genus of avian blood parasites, *Haemoproteus*. This chapter emphasises the risk that invasion of linear revegetation sites (e.g. along rivers and creeklines) and small plantings in the Midlands by noisy miners could pose, through the exclusion of other songbirds and perhaps through fitness effects on individuals that persist in their presence. The methodology used in this chapter could present a useful tool in determining how birds perceive habitat quality at restoration sites and in monitoring bird health.

Chapter 5

Vegetation structure and density of edge habitat moderate risk of predation on songbird nests in an agricultural landscape. An often-speculated mechanism of bird species decline in agricultural landscapes is higher levels of nest predation due to a greater abundance of mesopredators and a general loss of habitat structure. Early studies testing this hypothesis regularly used artificial nests, relied on identifying nest predators from indentations on plasticine eggs or "nest state" and employed statistical techniques that have since become outdated. In this chapter, I use motion-sensor cameras to monitor nests of two model songbird species, brown thornbills (*Acanthiza pusilla*) and superb fairy-wrens. Unlike other studies of nest predation in woodland birds, I monitored nests that were built both in

woodland remnants and isolated vegetation in the agricultural matrix. I used a nest-survival analysis and generalised linear models to test for relationships between daily survival rates of nests and surrounding habitat features (e.g. woodland cover, density of edge habitat, canopy closure) across multiple spatial scales. I also used a novel method – terrestrial LiDAR – to quantify vegetation structure at nesting sites. The results of this chapter suggest that small patches of revegetation in the Midlands could provide ideal breeding habitat for small-bodied songbirds because of an absence of larger nest predators. Having identified the primary nest predators in the Midlands, nesting sites that birds chose and patterns of nest survival, practitioners will be better positioned to provide safe nesting sites in restored habitats. Data collected using LiDAR provides future opportunities to compare structural attributes of nest locations selected by birds at restoration sites with those of birds living in reference habitat types.

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Chapter Two

Study System & Historical Perspectives

A Tasmanian wedge-tailed eagle (Aquila audax fleayi) watches over the Midlands.

The Tasmanian Midlands

The island of Tasmania (*c*. 65 000 km^2) lies at the southern-most tip of Australia between latitudes 40°- 44° South. Tasmania is separated from the Australian mainland by Bass Strait, a shallow and tempestuous 250 km stretch of water that provides an intermittent barrier by inundating the Bassian Plain, most recently about 14 000 years ago (Lambeck & Chappell 2001). This barrier has isolated much of Tasmania's terrestrial fauna from mainland Australia resulting in high levels of speciation, although 25 species of migratory bird regularly traverse Bass Strait (Chan 2001; Dingle 2004). These migrants include some small to medium-sized woodland birds that use King Island and islands of the Furneaux group to move between coasts (Fig. 2.1). In recent times, Bass Strait has also protected Tasmanian wildlife from the catastrophic impacts of the introduced red fox (*Vulpes vulpes*, McQuillan *et al.* 2009).

Tasmania has a temperate maritime climate with mean maximum temperatures of between 18°C and 23°C in summer and 9°C to 14°C in winter (ACE CRC 2010). Strong westerly winds known as the "roaring forties" are persistent throughout the year. This airstream and the mountainous topography of Tasmania's Central Plateau result in the heaviest rainfalls falling in the western half of the state (> 3000 mm annually) where the dominant vegetation types are moorland, wet sclerophyll forest (dominated by tall eucalypts with an understorey of broad-leaved shrubs and projected foliage cover of 30-70%) and temperate rainforest (dominated by *Nothofagus*, *Atherosperma*, *Eucryphia* and *Phyllocladus* with 70-100% crown cover, Jarman *et al.* 2005)). Most of these forests are protected in World Heritage listed reserves and so Tasmania has the highest proportion of remaining forest of all the Australian states and territories (46%, Bradshaw 2012).

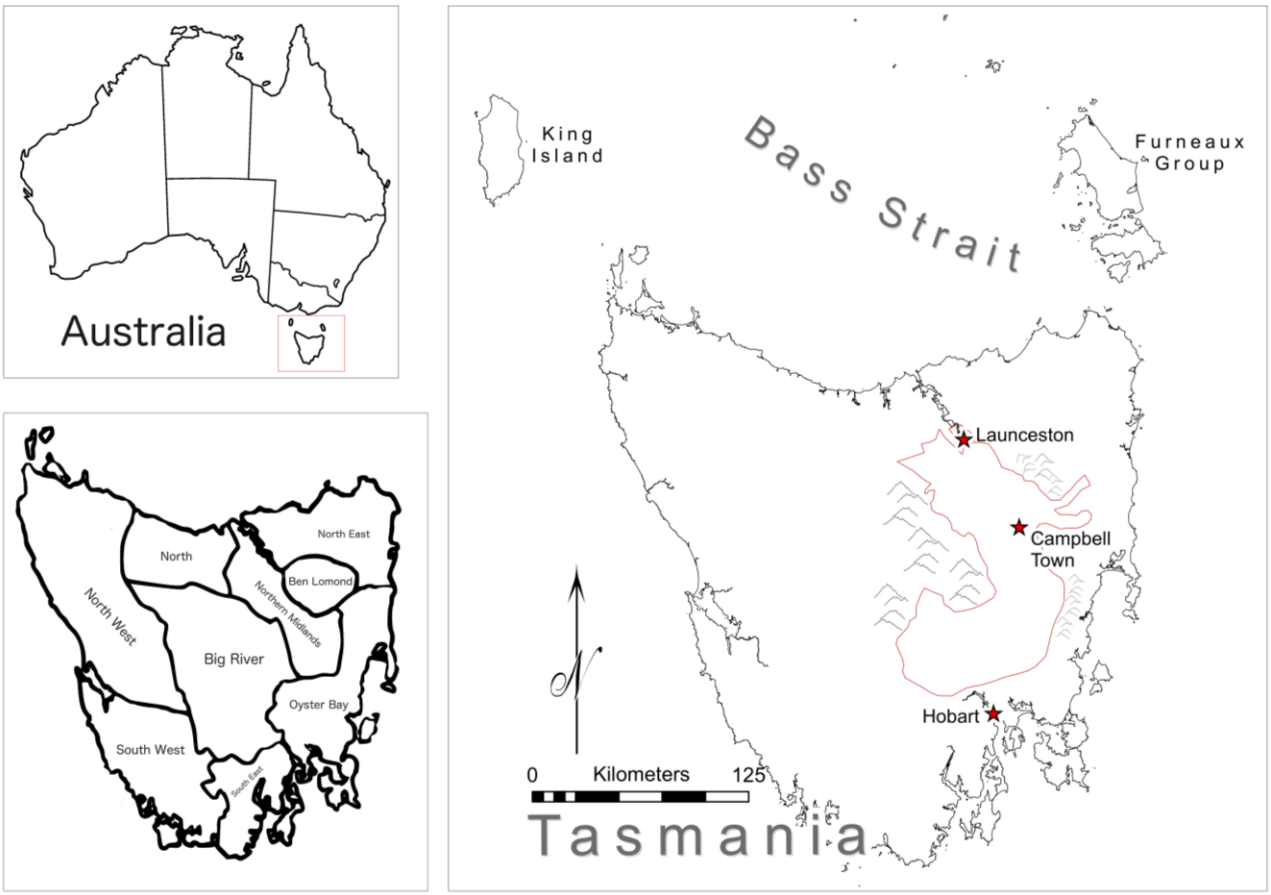

Figure 2.1. Location of the Midlands region (a.k.a. the "Midlands Duck", outlined in red) of Tasmania, Australia. I adopt the boundaries defined by the Midlands Biodiversity Hotspot and extend these to encompass the Northern Midlands interim bioregion (IBRA7 Region 12). *Bottom left*: Map of tribal divisions of Aboriginal people on mainland Tasmania, adapted from Johnson and McFarlane (2015).

In contrast, the lowland plains of the Tasmanian Midlands (hereafter the Midlands) lie in a rain shadow at the foothills of the Central Plateau and the Great Western Tiers and receive only between 500 mm and 600 mm of rainfall annually. The dry eucalypt woodlands (10-30% crown cover) of the Midlands are poorly represented in the conservation estate (4% of the region is protected, Duncan 2005). The aesthetic, cultural and ecological value of these woodlands are under-appreciated by local people when compared to Tasmania's wet forests. Less than 10% of the original woodland vegetation remains and less than 3% of

native grasslands (Jones & Davidson 2016). The critically endangered temperate grasslands of the Midlands are the most fragmented and depleted ecological community in Tasmania (DPIPWE 2010) but are of special significance to birds such as blue-winged parrots (*Neophema chrysostoma*) and quail species as an important source of food (seeds and an abundance of insect prey).

Agricultural intensification continues to result in habitat loss with many farmers clearing native vegetation and shelterbelts to install large pivot irrigation systems. One Midlands farmer alone installed seven centre pivot irrigators in 2018 with a total length of over 3 km and constructed an additional 5 km of underground water mains and 2 km of service roads. This typifies the rapid industrial development of the region. Such infrastructure represents the clearance of more than 900 hectares of native vegetation and pasture for the purpose of planting exotic crops. Prior *et al.* (2013) found high levels of contemporary tree loss in the Midlands due to accelerating rates of clearing but also a lack of recruitment and growth in existing trees. This will likely be exacerbated by the recent relaxation of Tasmania's land clearing laws; as of 2018, landowners can legally clear up to 40 ha of native woodland annually.

Birds of the Midlands

Despite a long history of anthropogenic modification (see *A historical perspective* below), the Midlands is recognised as one of 15 Australian Biodiversity Hotspots. At least 32 nationally threatened species and more than 180 plants and animals listed at the state government level are present in the region (Cowell *et al.* 2013). Woodland bird communities of Tasmania are of high biodiversity value. Around 200 species of birds regularly occur on the island, half of which can be considered terrestrial (birds living predominantly or entirely

on land) Ten of the islands twelve endemic birds can be found in the Midlands (Appendix A.1), although some species such as the strong-billed honeyeater (*Melithreptus validirostris*), black-headed honeyeater (*Melithreptus affinis*) and Tasmanian thornbill (*Acanthiza ewingii*) are more commonly recorded in the mesic forests of southern Tasmania. Many of the other local bird species are distinct from their counterparts on mainland Australia because of differences in plumage, vocalisations and migratory behaviours (BirdLife Australia 2016). It is important to conserve Tasmanian subspecies (e.g. Tasmanian wedge-tailed eagle *Aquila audax fleayi*, Tasmanian silvereye *Zosterops lateralis lateralis* & Tasmanian striated pardalote *Pardalotus striatus striatus*) because of their unique adaptations to the islands climatic and geographic characteristics. Only four birds found in the Midlands are listed as endangered at the state level (the grey goshawk *Accipiter novaehollandiae*, Tasmanian wedge-tailed eagle, Tasmanian masked owl *Tyto novaehollandiae castanops* and swift parrot *Lathamus discolor*) but very little information exists for population trends in most species.

Some birds listed as endangered or vulnerable in other Australian states are not recognised as threatened in Tasmania, such as the striated fieldwren (*Calamanthus fuliginosus*, endangered in NSW), scarlet robin (*Petroica boodang*), flame robin (*Petroica phoenicea*), white-fronted chat (*Epthianura albifrons*) and dusky woodswallow (*Artamus cyanopterus*, all vulnerable in NSW). This is concerning, given that some of these species are breeding migrants to Tasmania and recovery strategies currently fail to recognise this. If the governing threats facing these species are encountered during their breeding season in Tasmania, then recovery efforts on the Australian mainland could be in vain.

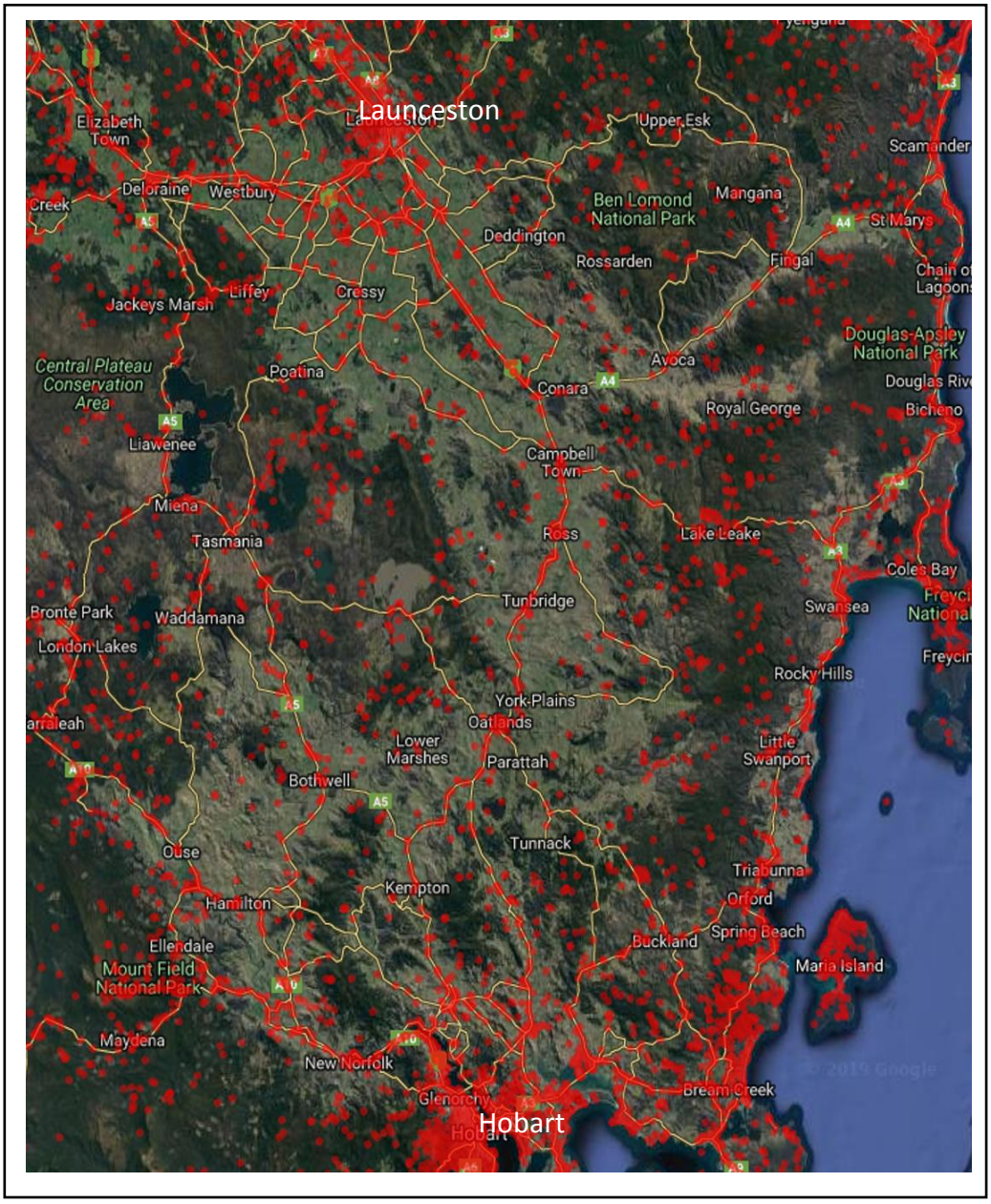

Figure 2.2. Occurrence records of all bird species in the Tasmanian Midlands (1990-2019) obtained from the Atlas of Living Australia (https://www.ala.org.au/). Observations made by citizen scientists are commonly used to establish trends in bird populations, but because the Midlands region is mostly privately owned such records are scarce. Of the few observations that are available, most are of birds situated along the Midland Highway that connects Tasmania's two major cities, Launceston and Hobart. This illustrates the need for further broadscale monitoring of birds on farms.

A historical perspective: changes in land use and bird communities

Aboriginal Tasmanians (Palawa) were the first land managers of the Midlands. Unfortunately, much of Tasmania's Aboriginal heritage has been lost and so very little is understood about how Indigenous peoples managed the land (Gammage 2011), let alone their relationships with birdlife. For example, it is only recently that researchers used artefact sites to examine where Palawa preferred to live and the vegetation types that they exploited (Jones et al. 2019). It is, however, generally accepted that Aboriginal peoples used fire to promote open grassy landscapes in the Midlands that were ideal for hunting game species including kangaroos and the now extinct Tasmanian emu (*Dromaius novaehollandiae diemenensis*, Gammage 2008; Romanin *et al.* 2016). Given the Tasmanian climate, some authors have noted that a larger proportion of Tasmania's vegetation might be expected to be rainforest rather than eucalypt forest, grassy or heathy woodlands (Gammage 2011). This, together with evidence for shifting boundaries of vegetation communities, could signal long-term and purposeful burning by Tasmanian Aboriginals (Gammage 2011). Three Aboriginal tribes occupied the Northern Midlands territory, including the Stoney Creek tribe (Tyerer.note.panner) based near Campbell Town (Fig. 2.1). The Southern Midlands and Central Highlands were occupied by the Oyster Bay and Big River Nations respectively (Johnson & McFarlane 2015).

In 1803, the British settled in southern Tasmania but rapidly occupied the Midlands region, which, after the Cumberland Plain in New South Wales is the second oldest agricultural landscape in Australia (Fensham 1989). The grassy woodlands of the Midlands appealed to colonial settlers because they were well suited to livestock grazing, naturally fertile, allowed for easy travel and required little effort to clear (Gammage 2008). Colonial

artist John Glover wrote of the region that, “It is possible almost every where, to drive a carriage as readily as in a Gentleman’s Park in England” (Glover 1835). A shipment of Merino rams arrived in 1820, by which time the plains of the Midlands were almost entirely privately owned. Agricultural expansion and livestock numbers increased exponentially thereafter; there were just 54 000 sheep in Tasmania in 1816 increasing to 553 698 head by 1826 (Johnson & McFarlane 2015).

Conflict between white pastoralists and Aboriginal peoples peaked during this time, and martial law was subsequently declared in 1828 (Johnson & McFarlane 2015). This led to what some have called the “Tasmanian Genocide” and the loss of Aboriginal peoples from the Midlands (Harman 2018)The widely spaced trees and open grasslands once maintained by Aboriginal Tasmanians are thought to have been replaced by more dense stands of vegetation in their absence. This is supported by a palaeoecological study of pollen and charcoal samples which indicated a dramatic increase in fire activity after European settlement and changes in the composition of woodlands, specifically a decline in *Allocasuarina* tree species (Romanin *et al.* 2016).

The Midlands has since experienced several waves of deforestation. As early as 1890, though, parliamentarian William Brown suggested that the establishment of an “arbour day, in conjunction with the free distribution of trees to landed proprietors, would add very materially to re-forest large areas” of what he called “treeless wastes”. Adding that, “many thousands of plants would be distributed to the now almost treeless Midland District” (HAJ no. 63, pg.7, TPP 1890). One of the most significant periods of land clearance occurred in the 1970s owing to commercial harvesting for the newly established woodchip industry (Prior *et al.* 2013). A crash in wool prices and the subsequent diversification of many farms

to more intensively managed crops led to secondary clearing of remnant woodlands in the 1990s (Prior *et al.* 2013).

Figure 2.3 *Top*: Landscape painting by colonial artist John Glover (1836) depicting Aboriginal people (already dispossessed of Tasmania's mainland) and open grassy woodlands near Deddington in the northeastern Midlands. "Mills' Plains, Ben Lomond, Ben Lodor and Ben Nevis in the distance", Tasmanian Museum and Art Gallery, Hobart. *Bottom*: Dead eucalypt trees that now characterise parts of the Midlands.

As irrigated lands expanded, small patches of woodland and scattered paddock trees were particularly vulnerable to clearing. Livestock grazing, soil compaction, outbreaks of phytophagous insects, the application of fertilisers (superphosphate) and sowing of exotic

pasture grasses also added stress to isolated paddock trees(Kirkpatrick *et al.* 1999). These pressures, combined with drought, have resulted in high levels of tree mortality and eucalypt dieback such that many Tasmanians now characterise the Midlands by its dead and dying trees (Fig. 2.3, Close & Davidson 2004). Wetlands too have suffered since European colonisation. At least 34% of wetland areas in the Midlands have been drained and a further 23% have experienced artificial changes in water level (Fensham & Kirkpatrick 1989).

Ten woodland bird species that have been introduced to Tasmania, either fortuitously (aviary escapees) or on purpose, are commonly recorded in the Midlands. Several other domestic species such as the Indian peafowl (*Pavo cristatus*) and common pheasant (*Phasianus colchicus*) are also present but rarely sighted. Many of these species are of European origin such as the common starling (introduced ~1880), European goldfinch (*Carduelis carduelis* ~1884), and house sparrow (Passer domesticus ~1869, Tasmanian News 1899), but others are native to mainland Australia (see Chapter Three). Grouse and partridge species failed to establish in the Midlands despite multiple introduction attempts (Tasmanian News 1899). The effects of these introductions on native bird populations are complex and poorly understood. Perhaps the best demonstration of an introduced species having unforeseen consequences on local avifauna concerns the European or common blackbird (*Turdus merula*).

Blackbirds have had a turbulent history in Tasmania since their first, albeit failed, introduction around 1827 (Lord 1933). It wasn't until the early part of the 20th century that blackbirds had established successfully and by 1930 they were present in significant numbers (Guiler 1989). Farmers and scientists alike were immediately concerned over the impact blackbirds would have on the fruit growing industry and so a bounty was introduced

in 1941. The same payment scheme was used as for bounties on the now extinct thylacine or Tasmanian tiger (*Thylacinus cynocephalus*) and by 1946, more than 79 000 birds and nearly 22 000 eggs had been destroyed (Guiler 1989). However, police recommended the discontinuance of payment for blackbird eggs in 1942 in order to discourage nest hunting which "destroyed the nests of, or otherwise disturbed the nesting of valuable native birds" (The Examiner 1942). In addition, the Gould League for the Protection of Birds in Tasmania (1944) said that the subsidy "increased the wilful destruction of birds at an alarming rate, and many of our native birds have been destroyed in the hunt for their heads". Blackbirds are common throughout the Midlands today, particularly in degraded patches of remnant woodland and near to urban areas.

Hunting of native birds for food, recreation, or because of their perception as agricultural pests is likely to have contributed significantly to the current composition of bird communities in the Midlands. Colonial settlers hunted native birds during periods of drought when crops failed and alternative sources of food were sought. Game species included the common bronzewing (*Phaps chalcoptera*) which was noted as "feeding in large quantities off the stubble and delicious to eat", the endemic green rosella (*Platycercus caledonicus*), quail (*Coturnix* spp.), the Tasmanian emu and black swan (*Cygnus atratus* the first bird species to be protected in Tasmania in 1804, Evans 2012). In his *History of Van Diemen's Land*, Bischoff (~1830) wrote, "The birds that may be called game are very numerous, with the exception of the emu". Indeed, emus were previously much more abundant, but were vulnerable to hunters when they moved into the plains where they foraged. A local chaplain commented in his diaries that his dog had "killed 141 kangaroos and 24 emews" in 1805 (The Voice 1933). The Tasmanian Emu went extinct around 1850. It

is unknown how this affected ecological communities, but emus may have played an important function in seed dispersal (McGrath & Bass 2016).

A Tasmanian endemic, the yellow wattlebird (*Anthochaera paradoxa*), was particularly sought after by shooters in the Midlands from early settlement up until the 1980s. The wattlebird was described as being "held in higher esteem for culinary purposes than any other bird that flies" and in a local newspaper the species "popularity as an article of food" was said to put "it in danger of extermination" (1910). The wattlebird was protected for two years in 1902 & 1903, but hunting resumed thereafter. Concern grew for the wattlebird's future such that in 1946 a request was made by the Tasmanian Field Naturalists' club to the Fauna Board to have wattlebirds protected once more. This was promptly rejected due to the species being the "best eating bird in the state" (The Mercury 1946). Historical accounts suggest there has been a massive decrease in the abundance of yellow wattlebirds. Landowners in the Midlands recalled hunting parties shooting hundreds of individuals on each trip as late as the 1970s (Gilfedder *et al.* 2003) but encountering such numbers of wattlebirds is unimaginable now.

Birds of prey were also regular targets of hunters and farmers. Wedge-tailed eagles, the largest raptors in Australia and among the largest in the world, were persecuted for their reputation as lamb killers (West 1852). One article describes an elaborate method that farmers used to capture eagles. A "stockade of logs" would be "constructed round the carcase of a sheep or lamb to a height of about three or four feet, with a similar measurement in length and width. The eagle, upon either seeing or smelling the sheep, naturally alights on the logs, and hops down inside the enclosure" but the eagle being "unable to rise abruptly from the ground, is a prisoner until the shepherd on his rounds

comes across him" (The Mercury 1923). The grey goshawk (*Accipiter novaehollandiae*) poses no threat to livestock but was nonetheless sought after as a trophy species because of its brilliant white plumage, described by one early settler as a "very great curiosity" (The Mercury 1933). The first record of a grey goshawk being killed may be from 1773, when explorers from one of Captain Cook's ships, the *Adventure*, "shot a large white fowl of the eagle kind, about the size of a kite" (Kerr 2004). It was noted that the goshawks "conspicuous appearance leads to its' being shot whenever it appears near civilisation" and by 1852 it was said that "the beautiful white hawk, once very abundant, is now becoming rare, having been nearly extirpated for the sake of its skin by the zeal of bird collectors" (West 1852). The grey goshawk is the only all-white raptor species in the world and, like the Tasmanian wedge-tailed eagle, has been listed as endangered under state legislation.

The threat of hunting to local bird populations was so pervasive that in 1942 the Fauna Board of Tasmania circulated 2000 charts illustrating which birds had value in destroying pests and included an appeal to the public to protect them (Examiner 1937). Around this time, the services that birds provide to agriculture began to be acknowledged. In a presentation to the Tasmanian Field Naturalists Club, it was said that the "honeyeating birds assured the future of timber supplies" while "offal-eaters freed man from plagues of blow-flies" (The Mercury 1934). The extinction of the passenger pigeon in North America prompted one Tasmanian to publish an article in the Hobart Daily Mail entitled "Extinct birds, a lesson to Tasmania" (Daily Post 1912), in which the following passage is relevant to this thesis: "It may be said by some exacting people that ornithology has nothing to do with agriculture. Take away the birds, and the farmer and orchardist would suffer to a very considerable extent. The feathered workers keep down destructive insects, worms, etc., and may lie described as culturist's army of unpaid toilers. A silent bush is bad enough but

remove the winged life from our cultivations and pastures and our troubles within the realm of agronomics would be increased a hundredfold. It is, however, a regrettable fact that many useful species of the feathered workers are disappearing in Australia, and we are presented with a sad example of Australian thoughtlessness."

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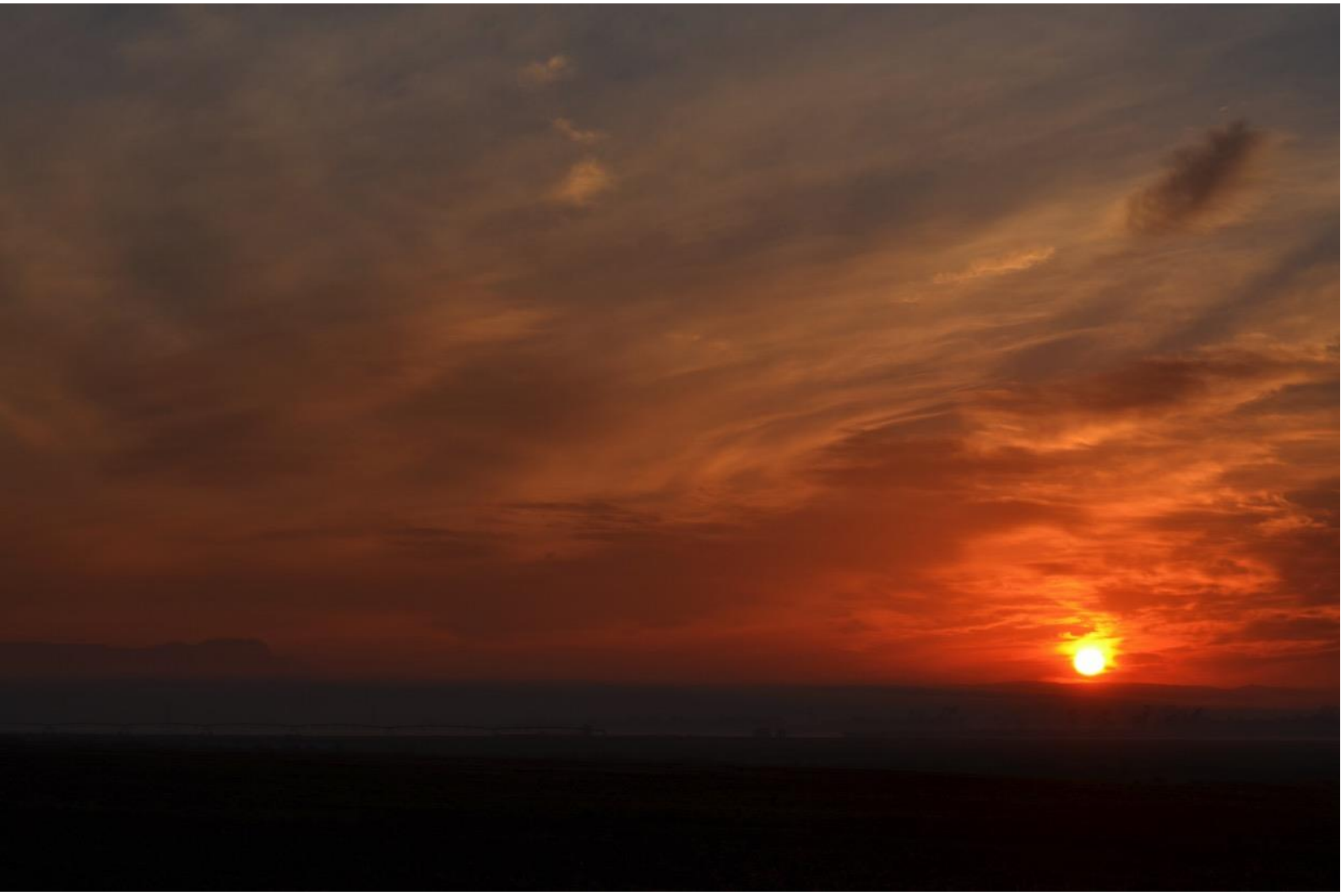
Chapter Three

Long-term change in bird communities of an agricultural landscape: declines in arboreal foragers, increases in large species



Sunrise in the north eastern Midlands. Ben Lomond (1572 m) on the left and a centre pivot irrigator in the foreground.

Abstract

Populations of many birds are declining in agricultural landscapes around the world. Mechanisms underlying these declines can be better understood by exploring population change in groups of species that share life-history traits. We investigated how land-use change has affected birds of the Tasmanian Midlands, one of Australia's oldest agricultural landscapes and the focus of an ambitious habitat restoration program. We surveyed birds at 72 sites, some of which were previously surveyed in 1996-1998, and tested relationships of current patterns of abundance and community composition to landscape and patch-level environmental characteristics. Woodland cover at survey sites, projective foliage cover, densities of a hyperaggressive honeyeater (the noisy miner *Manorina melanocephala*), landcover diversity, the elevation of survey sites and leaf litter cover all had significant effects on the composition of local bird communities. Fourth-corner modelling of relationships between species traits, abundance and environmental factors showed strong negative responses of aerial foragers and exotic bird species to increasing woodland cover. Arboreal foragers were positively associated with projective foliage cover and small-bodied birds were most negatively influenced by the presence of noisy miners. Analysis of change suggests an increase in large-bodied birds with a granivorous or carnivorous diet but declines in some arboreal foragers and nectarivores. Common species, including Tasmanian endemics, were among those with the largest proportional declines. Changes in species richness were best explained by changes in noisy miner abundance and levels of surrounding woodland cover. We encourage restoration practitioners to trial novel planting configurations that could be more resilient to invasion by noisy miners as well as a continued long-term monitoring effort such that the effects of future landscape change (revegetation or continued habitat loss) on Tasmanian bird communities can be examined.

Introduction

Agricultural intensification is a major cause of global biodiversity loss (Emmerson *et al.* 2016). Beyond the direct clearing and fragmentation of habitat that typically accompanies agriculture, farm management practices can modify wildlife communities through their effects on the abundance of food, shelter and predators. For example, rising levels of pesticide use to protect crops from herbivory has had wide-ranging negative impacts on invertebrate populations (Pisa *et al.* 2015) and has subsequently been implicated as a major contributor in the decline of farmland bird populations in Europe and North America (Boatman *et al.* 2004; Hallmann *et al.* 2014; Stanton *et al.* 2018). In contrast, corvids and mammalian mesopredators (for example feral cats *Felis catus* and raccoons *Procyon lotor*) are thought to have benefitted from an increased food supply on farms and fewer large predators (DeVault *et al.* 2011; Roos *et al.* 2018). The mechanisation of agriculture (i.e. tillage and weed control) and expansion of irrigated lands also results in the removal of discrete habitat elements such as paddock trees, surface rocks, coarse woody debris and hedgerows (Hunter *et al.* 2017b; Lecq *et al.* 2017). These features are often the only source of cover for animals in farm landscapes and are used by a range of taxa for breeding, thermoregulation and as sources of food (Fischer *et al.* 2010; Fitzsimons & Michael 2017; Denerley *et al.* 2018).

Understanding how land use affects wildlife communities is essential if we are to predict their response to future environmental change, whether that results from continued agricultural intensification or landscape restoration. This is especially important given the agricultural sectors need to meet a projected increase in global food demand of between 25 and 70% (Hunter *et al.* 2017a). Land-use change associated with agriculture can affect species differently according to their life-history traits such as body size, diet or dispersal

ability. Relationships between functional traits of species and population change can offer insight into the mechanisms by which land use affects wildlife (Langlands *et al.* 2011; Lindenmayer *et al.* 2018). This understanding can be applied to produce more targeted conservation strategies and may allow for broader approaches that protect several species at once (Hanspach *et al.* 2012; Howland *et al.* 2016). Functional traits can also be used to estimate the contribution of species to ecosystem services and, therefore, how those services might respond to land-use change (Bregman *et al.* 2016).

Birds have long been used as indicators of environmental condition and can be effective indicator species for the conservation of other threatened vertebrates (Bibby 1999; Ikin *et al.* 2016). They occupy many ecological niches, respond relatively rapidly to changes in habitat, are straightforward to monitor, and perform important ecological functions such as seed dispersal, pest control and pollination (Wenny *et al.* 2011). We surveyed birds in the Tasmanian Midlands, one of Australia's oldest agricultural landscapes, a National Biodiversity Hotspot and the focus of an ambitious habitat restoration program (Jones & Davidson 2016). The bird community of the Midlands has high biodiversity value, with ten Tasmanian endemic species and several distinct subspecies (Appendix A.1). Tasmania, more generally, is important for many species of terrestrial bird (at least 19) that migrate to the island from mainland Australia to breed each year (Chan 2001; Dingle 2004).

An increasing threat to local bird communities, as well as populations of other threatened vertebrates, is secondary clearing of remnant woodlands for the installation of large pivot irrigation systems (Prior *et al.* 2013; Gardiner *et al.* 2018). Agricultural fragmentation in the Midlands has also led to the behavioural and numerical dominance of a reverse keystone species, the noisy miner (*Manorina melanocephala*), in many small

patches of habitat (MacDonald & Kirkpatrick 2003); for a location to support a typical, diverse woodland bird community, noisy miners must be absent or at very low density (Piper & Catterall 2003). Noisy miners are native to Australia's eastern coast but have become overabundant (Maron *et al.* 2013). Their aggressive exclusion of small birds from suitable woodland habitat is listed as a *Key Threatening Process* under federal environment legislation (Department of the Environment and Energy 2019). The productive landscapes of the Midlands also support very high densities of feral cats which are a major predatory threat to birdlife, although it is unknown how mortality from cat predation might translate to population viability of birds (Woinarski *et al.* 2017; Hamer 2019).

Our first aim was to assess changes in the Midlands bird community over the past twenty years as a consequence of land-use change. The only broad-scale survey of birds in the Tasmanian Midlands was previously conducted in 1996-98 (hereafter the 1997 survey period, MacDonald & Kirkpatrick 2003). We repeated surveys at 34 historical study sites in order to explore the effects of habitat clearing, revegetation and changes in noisy miner abundance on bird communities. This will also help to identify particular species or functional groups of birds that should either be encouraged or discouraged by restoration efforts.

Second, we explored whether the response of birds to land-use change is trait-mediated. Previous research has identified ground-foraging insectivores as particularly vulnerable to habitat degradation and predation by introduced species in Australia (Ford *et al.* 2001). Nectarivores and large-bodied birds were also found to have declined in agricultural landscapes of New South Wales (Lindenmayer *et al.* 2018). Unfortunately, Tasmania lacks informative terrestrial bird survey data when compared to other parts of

Australia. This is particularly the case in the Midlands, which is mostly privately owned. To address this gap and provide context to the effects of land-use change, we described current patterns of bird abundance and community composition and how these are influenced by environmental factors. We use the results of our study to make practical recommendations for restoring habitat for terrestrial birds in Tasmania.

Methods

Study region

Tasmania lies at the southern-most tip of Australia and is separated from the Australian mainland by Bass Strait (250 km, Fig. 3.1). Islands of the Furneaux Group and King Island act as stopovers for birds that migrate to Tasmania in the spring and summer. The Midlands Biodiversity Hotspot (*c.* 8000 km^2) is defined by a low annual rainfall (< 600 mm) and lies within north (Macquarie and Esk Rivers) and south (Jordan, Clyde and Coal River) flowing catchments that are bordered by the mountainous Eastern and Western Tiers of Tasmania. Prior to European settlement, the Midlands consisted of grassy or heathy temperate eucalypt woodlands and native grasslands. More than 200 years of clearing for agriculture has left < 10% of native woodland and < 3% of native grasslands remaining (Jones & Davidson 2016). The region is now predominately exotic pastures for livestock grazing (primarily sheep), and crops of cereals, oilseeds and other high-value yields such as poppies for the pharmaceutical industry. Agricultural intensification continues to result in deforestation and particularly the loss of scattered paddock trees (Prior *et al.* 2013).

Temperatures range from mean daily maximums of 21.9 °C in summer and 11.4 °C in winter to mean minimum temperatures of 8.8 °C in summer and 1.9 °C in winter. However, Tasmania experienced several extreme weather events during our study, including a period

of drought in 2015, Tasmania's coldest winter in 50 years with abnormal snowfalls across the Midlands, followed by the warmest summer since records began and record levels of rainfall that caused significant flooding at some of our field sites (BOM 2018). Such extreme weather events, especially heatwaves, are expected to become more frequent in the Midlands under the effects of climate change (Bennett *et al.* 2010).

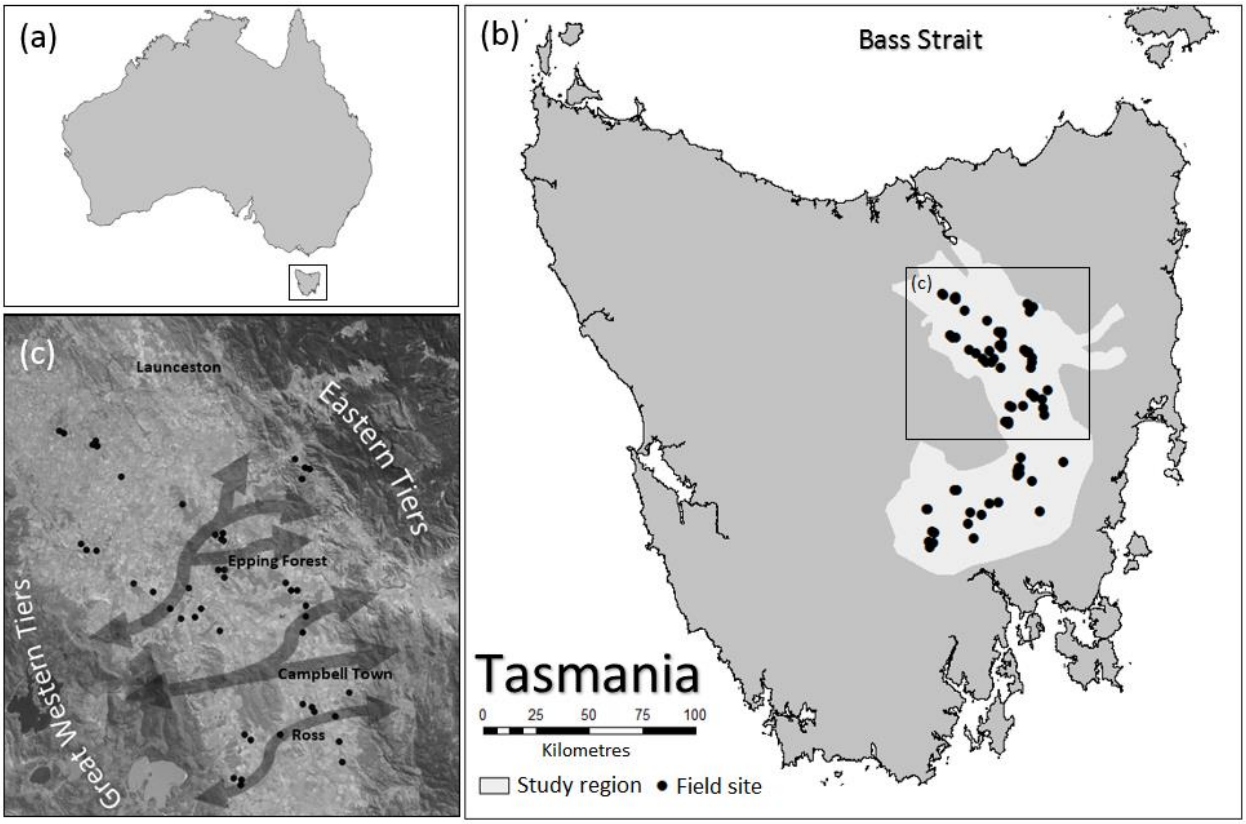


Figure 3.1. Location of survey sites in the Midlands of Tasmania, Australia. Inset (c) shows a satellite image of part of the study region, which is largely cleared of native vegetation. Arrows signify the conceptual east-west connections of the Midlands restoration program where revegetation is planned to occur. The "Ross connection" is currently being established with some sections of this corridor already five years of age.

Survey sites

We surveyed 72 sites representing the range of habitat types in the Midlands. This included 52 woodland remnants and five small (< 6 ha) mixed species eucalypt plantings, ranging in age since planting of approximately 20 to 30 years. To document birds that were using the agricultural matrix, we also surveyed 2-hectare sites that were placed *a priori* in five native grasslands, five pastures and five areas dominated by the exotic weed, gorse (*Ulex europaeus*). These sites usually included at least one paddock tree.

Remnant woodlands reflected a range of patch sizes and levels of modification: 15 small (0 - 20 hectares), 25 medium (20 - 200 hectares) and 12 large (> 200 hectares). The dominant tree species (canopy 10 - 30 m) were black peppermint (*Eucalyptus amygdalina)*, cabbage gum (*E. pauciflora)*, white gum (*E. viminalis)*, silver peppermint (*E. tenuiramis)* and gum-topped stringybark (*E. delegatensis)*. Typically, small and degraded patches of woodland were characterised by exotic pasture grasses throughout their interior, bracken fern (*Pteridium esculentum*) and introduced weeds including gorse and hawthorn (*Crataegus monogyna*). The midstorey of these patches was generally sparse.

Larger and less disturbed woodlands were more structurally complex with a greater diversity of low branching trees including wattles (*Acacia dealbata, A. mearnsii, A. axillaris*), sheoaks (*Allocasuarina verticillata, A. littoralis*), native cherry, (*Exocarpos cupressiformis*), yellow bottlebrush (*Callistemon pallidus*) and silver banksia (*Banksia marginata*). Dense thickets of prickly box (*Bursaria spinosa*) were common at some sites. The understorey of intact woodlands comprised of a patchy mosaic of heathy groundcovers (*Lissanthe strigosa, Epacris impressa*), bracken fern, native perennial grasses (*Themeda triandra*, *Poa*

labillardieri, *Austrostipa* spp.), sedges (*Lepidosperma* spp.) and rushes (*Juncus* spp.). Swards of spiny-head mat-rush (*Lomandra longifolia*) were a prominent feature at many sites.

Bird Surveys

Surveys were conducted by a single observer (GB) between May 2015 and February 2017 both at dawn and dusk (89% of surveys within three hours of sunrise). Surveys were undertaken blind as to the occupancy of species at field sites during the 1997 survey period. Each site was surveyed in clear weather on up to six occasions: twice during the non-breeding season (March-August) and twice each in spring (September-October) and summer (November-February). Due to limited farm access and flooding, not all sites could be surveyed six times. All sites were, however, surveyed in both winter and spring/summer to ensure that seasonal migrants were accounted for.

To enable a comparison with historical bird data, we repeated the survey methods of MacDonald and Kirkpatrick (2003). A 100 m wide fixed transect was placed parallel to the longest axis of the woodland and crossed from one side to the other (Fig. 3.2). For larger woodlands, transects began at one edge and extended 800 m into the interior. Each transect was further divided into 200 m segments (Fig. 3.2). Transects were walked at a constant pace with each segment surveyed for 10 minutes. All species detected by sight or sound were recorded, noting in which segment they occurred and their number. Birds that were heard but not detected on the transect were recorded as "*offsite*" and were not included in our final analysis. One historical survey site (Woodstock Lagoon) was excluded from all analyses of change in the bird community because it had become invaded by gorse such that it was no longer possible to walk a transect that was comparable to earlier surveys. At the conclusion of each transect survey, we also conducted a 2-hectare/20

minute bird survey (Loyn 1986) in the centre of each woodland and recorded birdsong for 20-60 minutes using an H2 Zoom acoustic recorder. We have not analysed recordings here, but they will contribute to future evaluations of species occupancy at our field sites, especially with the development of automatic song recognition software in Tasmania (Turner & Munks 2018).

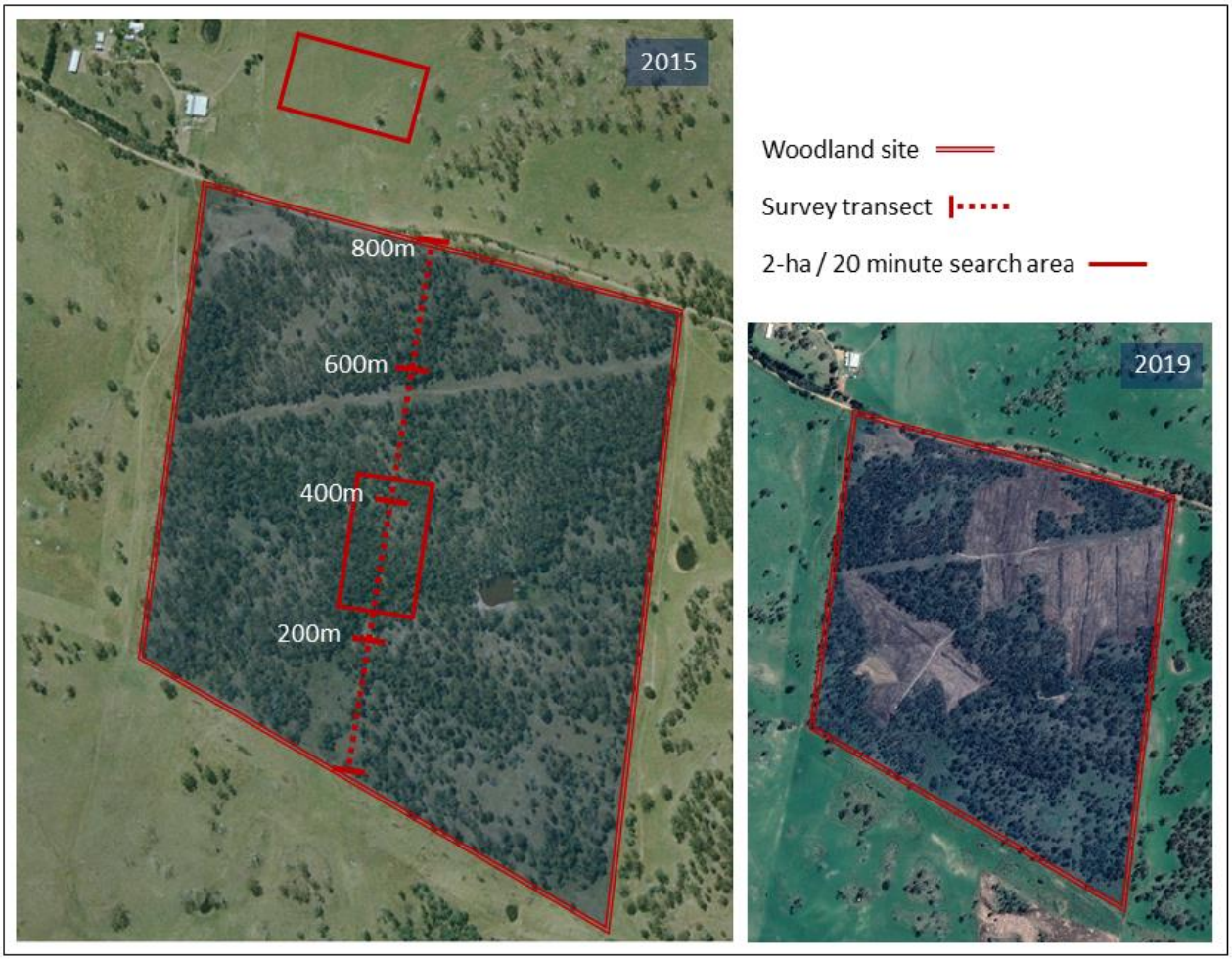


Figure 3.2 Aerial imagery showing a woodland remnant site (Tervue), the position of the survey transect and two 2-hectare survey areas, one in the woodland's interior and another in the adjacent pasture (i.e. a pasture site). Transects were divided into 200 metre segments and the segment in which a bird was detected during a transect survey was noted. At the end of 2018, this woodland site was partially cleared for livestock grazing (right).

Environmental Data

At the centre of woodland sites and plantings, we established two intersecting 10 m x 50 m plots and recorded the following site-scale attributes: the number of alive and dead stems (> 10 cm diameter at breast height, DBH), the DBH of alive and dead stems (cm) from which basal area was later calculated (m^2), average canopy height (m) and the summative length of fallen logs (> 10 cm in diameter, m). For analysis, these data were extrapolated beyond the sampling plot to be expressed per hectare. Environmental plots represented site-scale attributes of small to medium-sized habitat patches well, but we acknowledge that in large woodlands and on hillsides (where the vegetation was more heterogenous) these may not have captured the full range of habitat attributes available to birds. Plots were positioned on survey transects at the centre of woodlands and plantings to accommodate concurrent research on habitat use by mammals (Gardiner *et al.* 2018; Hamer 2019). A line-point intercept method (2 x 50 m transects) was used to estimate the percent cover of ground substrates which were classified into eight categories: leaf litter, bare earth, rocks, forbs and other low herbaceous plants, shrubs (> 30 cm in height, including bracken fern), sedges, mosses and lichen. Shannon's Diversity Index (H') was calculated to represent heterogeneity of groundcover (Forman & Godron 1986).

We used the software program ArcMap (version 10.4.1, ESRI 2019) to calculate the size (ha) and shape complexity of woodland remnants. Shape was calculated as the corrected perimeter to area ratio using the formula: $shape = \frac{perimeter\ of\ woodland}{\sqrt{4\pi(Area\ of\ woodland)}}$ (see Robertson *et al.* 2014). Satellite data and the geospatial layer, TASVEG 3.0 (DPIPWE 2013), were used to classify landcover within a circular buffer zone of one-kilometre radius that was centred on the middle of bird survey transects. TASVEG is a state government digital

map that depicts the extent of 162 vegetation communities in Tasmania (DPIPWE 2013). We updated the spatial layer to more accurately reflect vegetation composition at our survey sites, for example, where recent land clearing had occurred. For historical survey sites, patch size and landcover were also determined from digitised aerial images collected in 1997 to allow calculation of change between the 1997 and 2017 surveys. Seven categories of landcover were identified: (1) native eucalypt woodlands, including mixed eucalypt plantings; (2) native non-eucalypt woodlands; (3) productive eucalypt plantations; (4) pine (*Pinus radiata*) plantations; (5) agricultural pastures and other exotic vegetation; (6) open water (mostly farm dams); and (7) native grasslands (Table 3.1). Categories 1-4 were further classified as "woody vegetation". Cover of native grasslands could not be determined from aerial imagery, so for all analyses, the distribution of grasslands in 1997 was assumed to be unchanged from that in 2017. Shannon's Diversity Index was again used to represent heterogeneity of landcover.

Table 3.1. Summary of landcover types within 1 km of the centre of bird survey transects at woodland (n = 52) and planting sites (n = 5).

Land Cover Class	Mean % (standard deviation)	Min %	Max %
Eucalypt woodlands	35.3 (26.6)	0.2	96.5
Non-eucalypt woodlands	0.8 (0.4)	0.0	18.9
Eucalypt plantation	0.4 (2.7)	0.0	20.7
Pine plantation	0.4 (0.3)	0.0	17.0
Production agriculture	54.8 (3.8)	0.0	99.1
Native grassland	6.3 (1.6)	0.0	56.5
Open water	2.2 (0.6)	0.0	26.2

We counted the number of centre-pivot irrigation systems present within one kilometre of survey sites as a proxy for intensive land use. Pivot irrigators need relatively flat terrain to operate and usually require large areas of land (up to 300 ha in our study region)

to be entirely cleared of native vegetation. Climate data (mean annual rainfall, rainfall seasonality, mean annual temperature), as well as the elevation of survey sites and projective cover of woody foliage (Foliage Projective Cover, FPC) were derived from geospatial information systems (Xu & Hutchinson 2013; Gill *et al.* 2016). Values for FPC were averaged over the area of each transect. Finally, the density of noisy miners at survey sites was considered as an environmental variable because previous research has demonstrated strong effects of noisy miners on the abundance of other bird species (Thomson *et al.* 2015).

Table 3.2. Summary of trait variables used to explain variation across bird species in their response to environmental variables.

Trait	Category	Example Species
Body Size	Very Large (> 1000 g)	wedge-tailed eagle, Australian shelduck
	Large (100-1000 g)	sulphur-crested cockatoo, grey currawong
	Medium (25-100 g)	eastern rosella, fan-tailed cuckoo
	Small (< 25 g)	scarlet robin, superb fairy-wren
Diet	Invertebrates	Australian magpie, welcome swallow
	Vertebrates	brown falcon, nankeen kestrel
	Seeds & Grains	galah, house sparrow
	Nectar	musk lorikeet, eastern spinebill
	Plants	grey teal, Australian shelduck
	Generalists	black currawong, forest raven
Foraging Height	Terrestrial	flame robin, yellow-rumped thornbill
	Arboreal	striated pardalote, little wattlebird
	Arboreal / Terrestrial	grey-shrike thrush, grey butcherbird
	Aerial	welcome swallow, brown falcon
Movement Pattern	Resident / Sedentary	yellow-throated honeyeater, **grey butcherbird**
	Migratory *	silvereye, dusky woodswallow
	Nomadic ǂ	crescent honeyeater, musk lorikeet
Native Status	Native to Tasmania	green rosella, spotted pardalote
	Exotic to Australia	common starling, European goldfinch
	Introduced to Tasmania	laughing kookaburra, little corella

* Migratory species included only those birds known to migrate to mainland Australia annually, including partial migrants. ǂ Nomadic species also included altitudinal migrants and species described as dispersive in the literature.

Trait Data

All birds observed were categorised according to species traits (Appendix A.1) using data extracted from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant & Higgins 1990, 1993; Higgins & Davies 1996; Higgins 1999; Higgins *et al.* 2001; Higgins & Peter 2002; Higgins *et al.* 2006). These traits were body size, diet, foraging height, native status, and movement pattern (Table 3.2). We acknowledge that many species do not exclusively fit one category type for each trait, but for the purposes of analysis, birds were categorised according to their primary modes.

Statistical Analyses

Our analysis was performed in five stages. First, we used the package *BORAL* in R to produce a model-based unconstrained ordination of bird-count data for the visualisation of species-site relationships (Hui & Poisot 2016; R Development Core Team 2017). In all analyses of multivariate data, we pooled observations of birds from transect surveys at each site and specified a negative binomial distribution. We included a fixed row effect when generating our ordination to account for differences in the total abundance of birds at survey sites such that the resulting ordination reflects species composition.

Next, we used the package *mvabund* (version 3.13.1) to test for effects of environmental variables on bird community composition at survey sites (Wang *et al.* 2012). Candidate environmental variables were reduced to a final set of 10 (Table 3.3) by generating a correlation matrix (Spearman's rank) and eliminating those variables that demonstrated high levels of collinearity ($r_s > 0.6$). Woody vegetation cover and distance to the nearest patch of woodland ($r_s = 0.71$) were associated; only woody vegetation cover was retained in our models. Elevation and FPC were considered as representative of climatic

variables (e.g. mean temperature, rainfall seasonality) because these too were highly correlated.

Mvabund implements a generalised linear model (GLM) framework to analyse multivariate abundance data and fits a separate GLM to each species. This technique accounts better for the mean-variance relationship of count data than do distance-based multivariate analyses (e.g. canonical correspondence analysis) and allows formal tests of bird responses to environmental variables at both the community and species-specific levels (Wang *et al.* 2012). An offset (area of transect in hectares log-transformed) was used in our model to adjust for differences in the area surveyed at each site and the effort (total number of surveys log-transformed) argument was included to account for variation in the number of times a site was surveyed. Wald test statistics and *p*-values were determined from 999 resampling iterations via the PIT-trap method. Adjusted univariate *p*-values were calculated for individual species to test for their response to environmental variables.

We then used the *traitglm* function in *mvabund* to evaluate how bird species' traits influence their relative abundance and response to environmental variables (Warton *et al.* 2015). This method also uses an extension of a GLM, fitting a single predictive model to all species across all sites simultaneously. Three matrices of environmental data, species-abundance data and species-trait data were used to calculate a fourth matrix of trait-environment interaction coefficients, or 'fourth-corner' terms (Brown *et al.* 2014). For visual interpretation, we generated a heat-map of the standardised coefficients and used the LASSO penalty to remove all interactions that failed to improve model fit (Brown *et al.* 2014). We also used *traitglm* to model bird count data without specifying a trait matrix. This method effectively fits a multivariate species distribution model and assumes a different

environmental response for each species. Unfortunately, *mvabund* does not support the use of offsets when modelling fourth-corner problems. Therefore, while the results of this analysis remain informative, they do not account for differences in the area of each transect surveyed.

In our fourth analysis, we used GLMs to assess which elements of landscape change best-explained differences in species richness at historical survey sites between the 1997 and 2017 survey periods. A Poisson distribution of errors is usually assumed in models of discrete count data, but in this case, the response variable could be both positive and negative (species richness may have increased or declined). After examination of diagnostic plots, we found that a Gaussian distribution with identity link provided a good fit to our data. In these models we included combinations of the following explanatory variables: patch size (ha in 1997), change in patch size (ha), percent change in the amount of woody vegetation cover within one kilometre, change in noisy miner density (miners hectare^{-1}) and the number of pivot irrigation systems within one kilometre in 2017. We used an information theoretic approach to assess model performance and ranked models by Akaike's information criterion corrected for a small sample size (AICc, Burnham *et al.* 2010).

Finally, we used the log-response ratio (lnRR) to assess changes in species densities at historical survey sites. This was calculated as $\ln(\bar{x}^1/\bar{x}^2)$, where $\bar{x}^1$ was the mean density of a species in the 2017 survey period across all sites where that species was present (in any survey year) and $\bar{x}^2$ was the equivalent but for the 1997 survey period. Bird species with a low absolute density might still have a high lnRR because this measure reflects proportionate change. The lnRR was also used to assess changes in the density of birds that shared species traits. Here, $\bar{x}^1$ and $\bar{x}^2$ were the mean densities of all species present in a

trait category in the 2017 and 1997 survey periods respectively. Mean ± standard error is reported where appropriate.

Results

A total of 91 species was recorded across all our bird surveys (Appendix A.1). Of these, 72 were recorded during transect surveys, including five species that are exotic to Australia and three that have been introduced to Tasmania from the Australian mainland. Seven additional species were detected and identified from calls offsite, eight more were observed during 2 ha surveys in woodlands and four were found only in either pastures or grasslands (Appendix A.1). These additional records tended to be of birds that were rare (e.g. peregrine falcon *Falco peregrinus*), flying overhead (e.g. silver gull *Chroicocephalus novaehollandiae*), more typical of open habitats (e.g. striated fieldwren *Calamanthus fuliginosus*, banded lapwing *Vanellus tricolor*), or of domesticated birds and feral species with large aural detection distances (e.g. helmeted guineafowl *Numida meleagris*, Indian peafowl *Pavo cristatus*).

The size and type of habitat patch surveyed was related to community composition and species richness of birds. Species richness of native birds was highest for large remnant woodlands (23.09 ± 1.07), followed by medium (19.75 ± 1.35) and small remnants (14.47 ± 1.60), areas of gorse (12.5 ± 0.5), native grasslands (11.5 ± 1.77), plantings (10.6 ± 1.08) and pastures (7.25 ± 1.03). Because of the influence of noisy miners and a greater range in patch size, woodlands classed as medium size varied greatly in bird community composition (Fig. 3.3). Some medium-sized remnants supported species that were typical of large intact woodlands, while others were most similar in species composition to small and degraded remnants. Thus, when species were pooled across sites, medium remnants were the most

species-rich (58 species, *n* = 25) followed by large (52, *n* = 12) and small remnants (48, *n* = 15), native grasslands (31), plantings (25), gorse (23) and pastures (20).

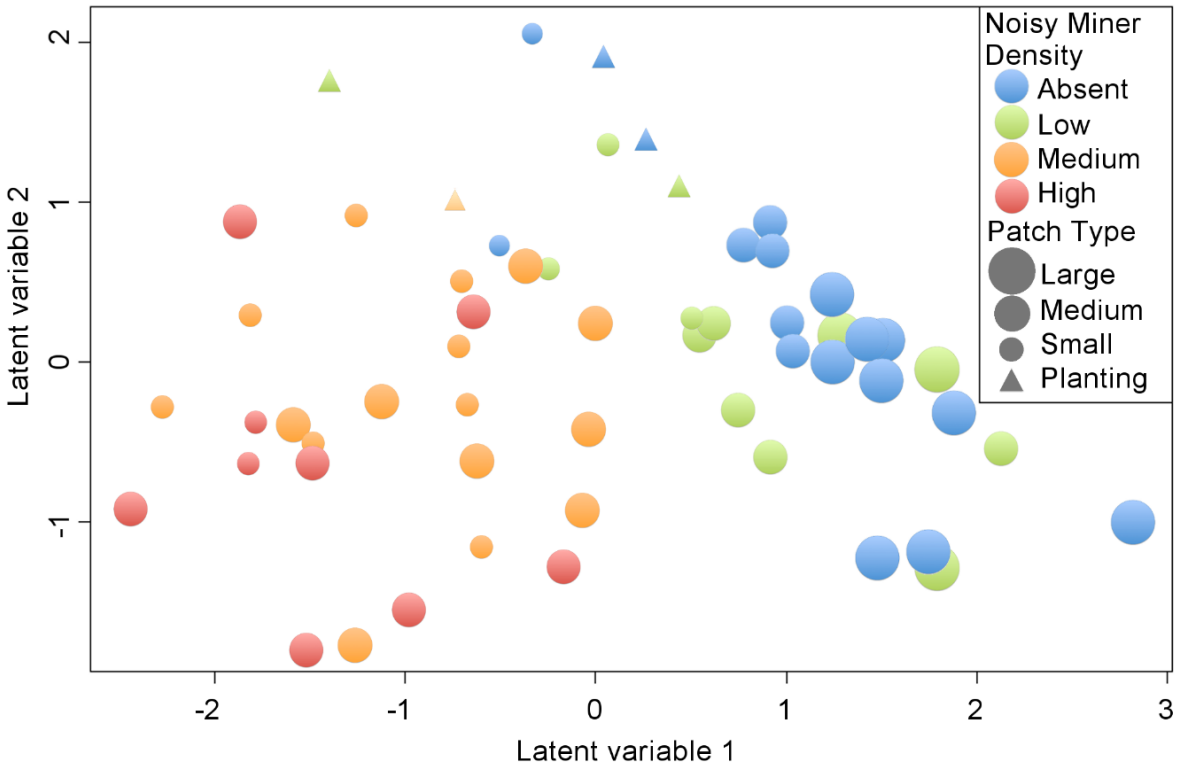


Figure 3.3. An unconstrained ordination of the bird community at woodland remnants (circles) and planting sites (triangles). Colours signify low (< 0.6), medium (0.6-2) and high (> 2) noisy miner densities (miners hectare-1). Large (> 200 ha), medium (20-200 ha) and small (< 20 ha) patches are indicated by the size of data points.

A variety of bird species used non-woodland habitats and some small patches of woodland had very high bird densities. Many of the birds that we recorded in pastures, grasslands and gorse were observed flying between nearby patches of woodland and used paddock trees within our survey plots as 'stepping stones'. Some species were more frequently recorded in these habitat types. For example, white-fronted chats (*Epthianura albifrons*) were most often seen in areas of gorse, and tree martins (*Petrochelidon nigricans*) were consistently recorded in those grassland and pasture sites where large paddock trees were present. Bird densities (birds hectare^{-1}, pooling species) were higher in small remnants

(8.70 ± 0.87) and plantings (7.01 ± 1.56) than in medium (6.70 ± 0.70) and large remnants (5.04 ± 1.00, X^2 = 8.25, *df* = 3, *p* = 0.04). This pattern was largely the result of a higher abundance of small-bodied and often introduced species (e.g. greenfinch *Chloris chloris*, house sparrow *Passer domesticus*, and common starling *Sturnus vulgaris*) in small remnants and plantings.

Relationships between environmental variables and the bird community

Bird-community composition was significantly influenced by six of the ten environmental variables that we examined (Table 3.3). Woody vegetation cover had the strongest effect, followed by FPC, density of noisy miners, landcover diversity, elevation and the percent cover of leaf litter. Fifteen species responded significantly ($p < 0.05$) to increasing cover of woody vegetation. Of these, six responded negatively and nine species, including three that are endemic to Tasmania, responded positively (Table 3.3). Univariate tests showed that no individual species contributed significantly to the effects of FPC and the cover of leaf litter on the multivariate bird community. Increasing density of noisy miners negatively affected seven small-bodied birds (< 25 g) but was positively associated with two species, the Australian magpie (*Cracticus tibicen*) and eastern rosella (*Platycercus eximius*). Despite elevation having a strong effect at the community level, the grey fantail (*Rhipidura albiscapa*) was the only species to respond significantly negatively in univariate tests (Table 3.3), although black-headed honeyeaters (*Melithreptus affinis*) tended to be more common in woodlands at higher elevations ($p = 0.072$).

Table 3.3. Summary of a multivariate analysis (manyGLM) testing for the effects of environmental variables on bird community composition. p-values (< 0.05 bolded) and Wald statistics are given for the effect of variables at the community level. Estimates ± standard error are for individual species that contributed significantly to the variance in community composition. The sign of the estimate (positive or negative) indicates the direction of a species response to the environmental variable.

Environmental Variable	Wald (1 *df*)	Community *p* value	Species where $p < 0.05$	estimate ± se
Woody Vegetation Cover	20.95	**0.001**	Australian magpie (*Cracticus tibicen*)	-0.015 ± 0.007
			common starling (*Sturnus vulgaris*)	-0.029 ± 0.006
			eastern rosella (*Platycercus eximius*)	-0.031 ± 0.012
			European goldfinch (*Carduelis carduelis*)	-0.037 ± 0.008
			forest raven (*Corvus tasmanicus*)	-0.010 ± 0.005
			grey butcherbird (*Cracticus torquatus*)	-0.019 ± 0.006
			black-headed honeyeater (*Melithreptus affinis*)	+0.053 ± 0.048
			crescent honeyeater (*Phylidonyris pyrrhopterus*)	+0.034 ± 0.013
			eastern spinebill (*Acanthorhynchus tenuirostris*)	+0.095 ± 0.033
			fan-tailed cuckoo (*Cacomantis flabelliformis*)	+0.058 ± 0.034
			grey currawong (*Strepera versicolor*)	+0.039 ± 0.013
			grey shrike-thrush (*Colluricincla harmonica*)	+0.064 ± 0.017
			scarlet robin (*Petroica boodang*)	+0.020 ± 0.006
			yellow wattlebird (*Anthochaera paradoxa*)	+0.044 ± 0.008
			yellow-throated honeyeater (*Lichenostomus flavicollis*)	+0.013 ± 0.010
Foliage Projective Cover	13.59	**0.011**	-	-
Miner Density	21.03	**0.012**	brown thornbill (*Acanthiza pusilla*)	-1.033 ± 0.189
			European goldfinch (*Carduelis carduelis*)	-1.394 ± 0.238
			grey fantail (*Rhipidura albiscapa*)	-0.952 ± 0.179
			scarlet robin (*Petroica boodang*)	-1.481 ± 0.378
			silvereye (*Zosterops lateralis*)	-3.096 ± 0.683
			superb fairy-wren (*Malurus cyaneus*)	-1.033 ± 0.222
			yellow-rumped thornbill (*Acanthiza chrysorrhoa*)	-2.590 ± 0.504
			Australian magpie (*Cracticus tibicen*)	+0.865 ± 0.129
			eastern rosella (*Platycercus eximius*)	+1.738 ± 0.217
Landcover Diversity H’	11.56	**0.013**	-	-
Elevation	13.65	**0.014**	grey fantail (*Rhipidura albiscapa*)	-0.006 ± 0.001
Leaf Litter Cover	10.61	**0.039**	-	-
Basal Area	9.95	0.088	-	-
Corrected Perimeter:Area Ratio	12.23	0.118	-	-
Canopy Height	9.57	0.468	-	-
Groundcover Diversity H’	8.74	0.546	-	-

Life-history traits of birds explained their response to environmental variables. The negative influence of noisy miners on small birds was once again highlighted by our trait analysis (Fig. 3.4). Large birds showed no response to miner density but were more common at lower elevations and at sites with a greater diversity of surrounding landcover types. The positive association between miners and birds introduced to Tasmania reflects a higher abundance of little and long-billed corellas (*Cacatua sanguinea*, *Cacatua tenuirostris*) and laughing kookaburras (*Dacelo novaeguineae*) in miner-dominated woodlands (Fig 3.4). These three species have been introduced to Tasmania from elsewhere in Australia. However, species exotic to Australia were negatively associated with miners. Exotic species also showed a strong negative response to increasing cover of woody vegetation and were more common in woodlands with a greater perimeter-area ratio (i.e. shape) and where the basal area of tree stands was high.

The diet and foraging habits of birds also moderated their response to environmental variables (Fig. 3.4). Arboreal foragers were more abundant at sites with greater FPC, more leaf litter and at higher elevations. Aerial foragers were negatively associated with woody vegetation cover and preferred sites with a more diverse composition of surrounding landcover. Aerial foragers were also associated with woodlands that had a simplified groundcover and a higher perimeter-area ratio. Birds with a mainly granivorous diet were more common in woodlands at lower elevations and where FPC and woody vegetation cover were low. In contrast, generalists and nectarivores were more abundant with increasing cover of woody vegetation.

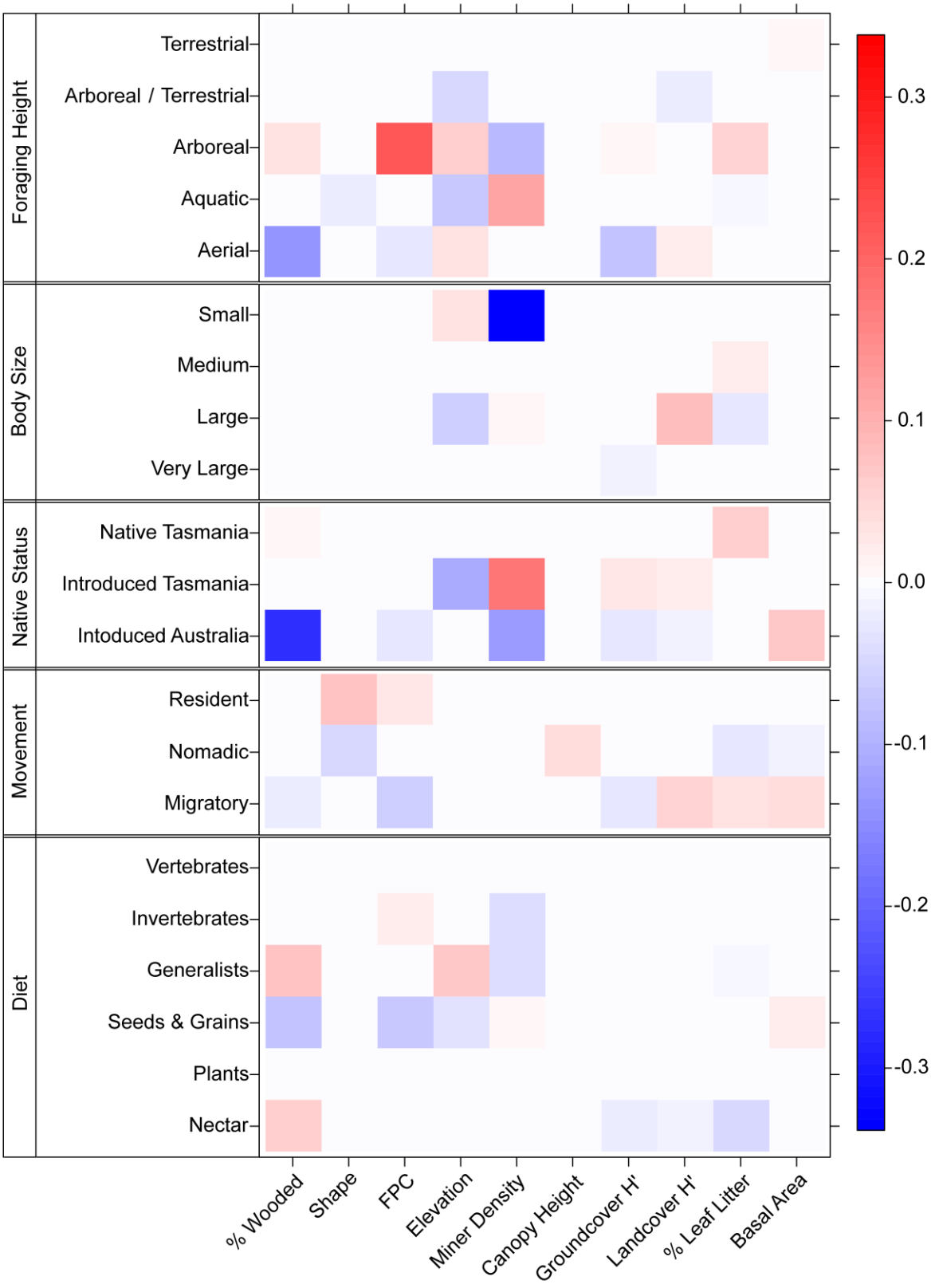


Figure 3.4. The relationship between birds that share species traits and environmental variables. Colours represent the strength of interactions (shading) and their direction (blue = negative & red = positive). The scale bar indicates the values of fourth-corner coefficients.

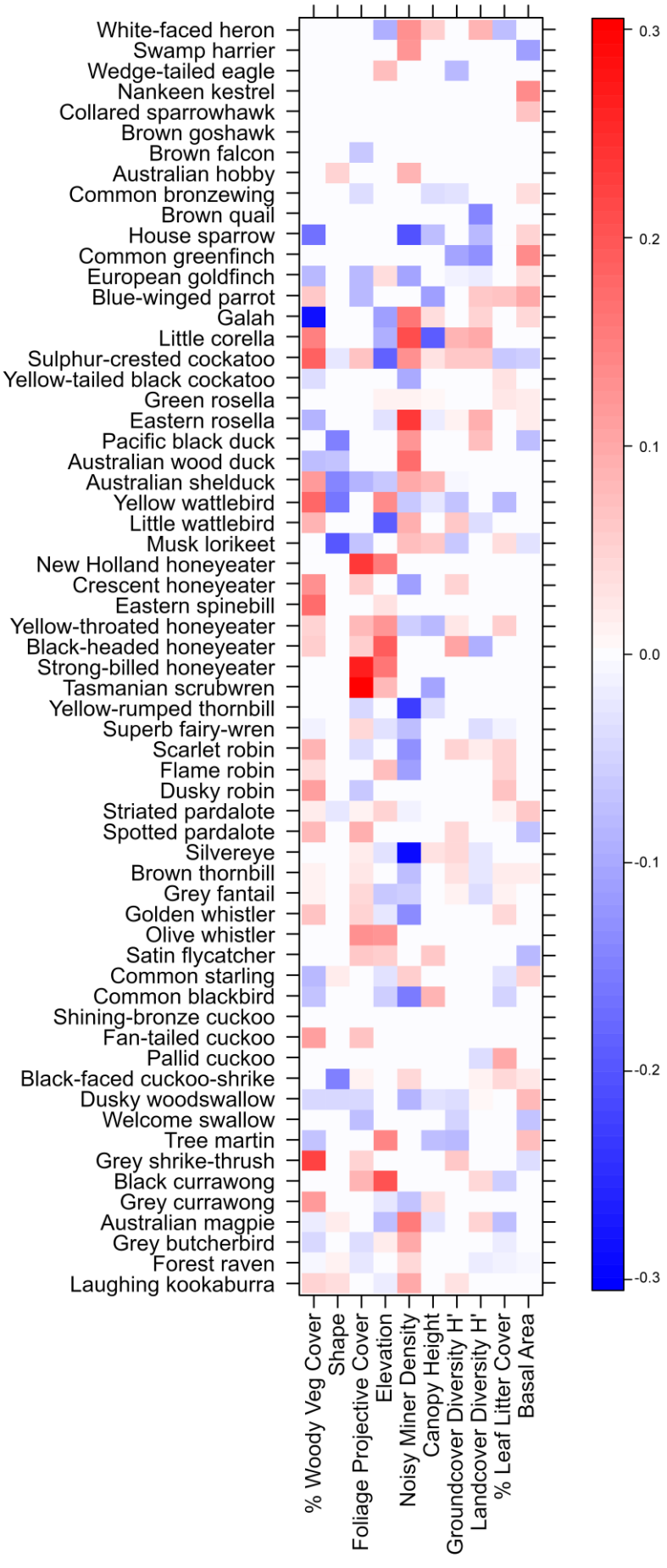


Figure 3.5. Relationships between bird species abundance and environmental variables. Species are ordered based on their diet. Colours represent the strength of interactions (shading) and their direction (blue = negative & red = positive). The scale bar indicates the values of fourth-corner coefficients.

Our species distribution model indicates more complex relationships between environmental variables and individual species (Fig. 3.5). For example, sulphur-crested cockatoos (*Cacatua galerita*) were more likely to be found in areas of high woodland cover but also preferred higher landcover diversity, higher groundcover diversity and woodlands with less leaf litter. This apparently inconsistent relationship could reflect the movement of cockatoos between large woodland sites where they were frequently observed during the day and smaller satellite patches of degraded woodland where they foraged in the morning and evening. Welcome swallows (*Hirundo neoxena*), swamp harriers (*Circus approximans*) and tree martins (*Petrochelidon nigricans*) were positively associated with shape and landcover diversity, which could reflect the preference of these species to forage in edge habitat near to open water and native grasslands.

Models of change in species richness

Changes in species richness at historical survey sites were related to changes in woodland cover and densities of noisy miners. Overall, though, there was generally little change in native species richness (-1.48 ± 1.2, range = 0 to 18) with nearly half of all sites (15/33) gaining or losing fewer than two species (Appendix A.2). The most parsimonious models (Δ AICc < 7 units, Burnham *et al.* 2010) explaining these changes always included the effects of change in noisy miner density (Table 3.4). Sites where noisy miners had increased in number were more likely to have experienced a decline in native species richness. Change in woody vegetation cover was also a significant predictor: sites that had a decline in surrounding woody vegetation also experienced a decline in species richness. The initial size of the woodland patch had a smaller effect on change in species richness, but larger patches tended to have fewer species recorded than previously (Appendix A.3 and A.4). The best model included just these three predictors and explained 45% (Adj. R^2) of the variation in

the net change in species richness. The top 3 models, however, were all within two Δ AIC*c* units and carried 38%, 23% and 16% of the weight respectively (Table 3.4).

Only three survey sites experienced a reduction in patch size from clearing. Thus, our analysis may not have had sufficient power to detect any effects of change in patch size on species richness. The number of pivot irrigation systems increased dramatically between 1997, when there was a total of just three pivot irrigation systems within 1 km of two of our survey sites, and 2017 when there were 33 irrigators near to 12 survey sites, but there was no relationship between the number of nearby irrigation systems and changes in species richness.

Table 3.4. Regression analysis of the relationship between the net change in native species richness at historical survey sites (n = 33) and changes in noisy miner density, woody vegetation cover and patch size. Also included as covariates were the initial size of the woodland patch surveyed and the number of pivot irrigation systems present within 1 km of the survey site in 2017. Models are ranked by AICc. See Appendix A.3 for models with W < 0.10.

Δ Native Species Richness							
AIC*c*	Δ AIC*c*	*W*	Δ Noisy Miner Density	Δ Woody Vegetation Cover	Patch Size	Δ Patch Size	Pivot Irrigators
210.36	0.00	0.38	-5.456 ± 1.369	0.378 ± 0.180	0.004 ± 0.002	-	-
211.34	0.98	0.23	-5.286 ± 1.422	0.380 ± 0.187	-	-	-
212.07	1.71	0.16	-5.857 ± 1.417	0.424 ± 0.185	0.004 ± 0.002	0.247 ± 0.233	-
212.97	2.61	0.10	-5.941 ± 1.452	-	-	-	-

Change in densities of noisy miners was highly variable between sites (range = -1.30 to +1.43 hectare^{-1}) but the mean density of noisy miners at historical study sites was lower in the 2017 survey period (-0.24 ± 0.12 hectare^{-1}). Noisy miners could be a candidate for

observer variation between survey periods, but we think this is unlikely given the species is easily detectable. Miners were recorded at 31/33 sites in 1997 and at 28/33 sites in 2017. Four woodlands had miners present in 1997 but no miners in 2017, including one site where miner density was previously as high as 1.21 miners hectare^{-1}. Miners were recorded at only one site where they were formerly absent and at a very low density (0.02 miners hectare^{-1}).

Woody vegetation cover had changed at 14/33 sites. At 12 of these, woodland cover had declined with an average loss of 3% (range = 1 to 8%). Native woodland was replaced by agricultural pastures and exotic vegetation at 11 sites and by both open water (farm dam) and pasture at one location.Two small remnants experienced an increase in surrounding woody vegetation cover, due to the establishment of a pine plantation near one site (+17%) and a productive eucalypt plantation at the other (+21%). In the woodland remnant adjacent to the eucalypt plantation, native species richness more than doubled from 12 to 30 species (3 additional species were heard offsite). Noisy miner densities at this site were also one-third of what they were previously (1.86 *versus* 0.56 miners hectare^{-1}). Only a narrow road separated one edge of the remnant from the eucalypt plantation and several birds were observed crossing between the two habitat types. The result was a community that combined many species more typical of large woodland remnants (e.g. pallid cuckoo *Cacomantis pallidus*, scarlet robin *Petroica boodang*) as well as those common to small sites (e.g. noisy miners & grey butcherbirds *Cracticus torquatus*). In fact, the bird community appeared to change between the first segment (0-200 m) of the transect, which was nearest to the plantation (25 species observed), and the second segment (200-400 m, 13 species). In contrast, the pine plantation had no effect on species richness, which was the same (10 species) in the nearby woodland remnant for both survey periods.

At the other extreme, native species richness more than halved at one medium-sized remnant (88 ha) from 31 species to just 13. The reasons for this change are not immediately clear, but noisy miner density at the site was much higher in 2017 than had previously been recorded (0.56 *versus* 1.75 miners hectare^{-1}, Appendix A.4). Landcover at this site was unchanged but the property manager had begun using a small area in the centre of the woodland for disposing of farm waste.

Changes in abundance

Birds associated with water (e.g. swamp harrier, white-faced heron *Egretta novaehollandiae*, Australian shelduck *Tadorna tadornoides*) were more abundant in the 2017 survey period (Fig. 3.6). This was also reflected in the lnRR of birds with a herbivorous diet and very large body size, which were mostly species of ducks (Fig. 3.7). Granivorous and raptorial birds also appeared to be more common. Swamp harriers had the highest proportionate increase among species for which lnRR was calculated, followed by galahs (*Eolophus roseicapillus*) and the little wattlebird (*Anthochaera chrysoptera*), a species common in urban environments of Tasmania. Sulphur-crested cockatoos and the introduced common starling had the greatest absolute increases in density: 0.26 to 1.11 cockatoos hectare^{-1} and 1.25 to 1.87 starlings hectare^{-1}. Forest ravens (*Corvus tasmanicus*) were also more abundant and, as in the 1997 survey period, this species was recorded at every survey site.

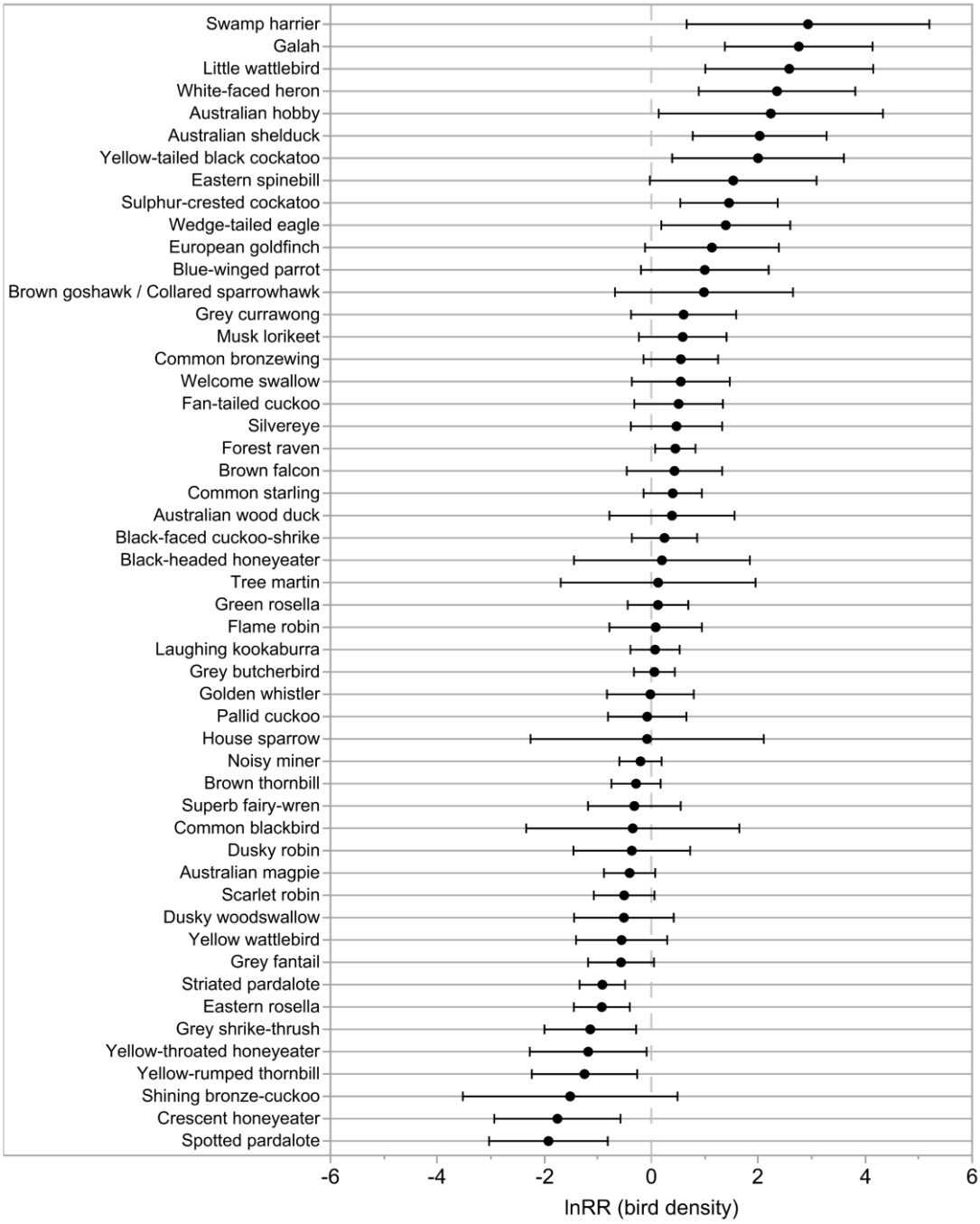


Figure 3.6. Changes in the mean density of bird species in remnant woodlands (*n* = 33) between the 1997 and 2017 survey periods. Positive values of the log response ratio (lnRR) indicate greater abundance in 2017 while negative values indicate greater abundance in the 1997 survey period. Differences are significant when 95% CI error bars do not overlap zero. Only those species that were recorded at more than one site and for which more than 5 individuals were observed are included. The lnRR could not be calculated for species that were recorded in only one of the two survey periods (e.g. satin flycatcher, little and long-billed corellas) and so these birds were also excluded.

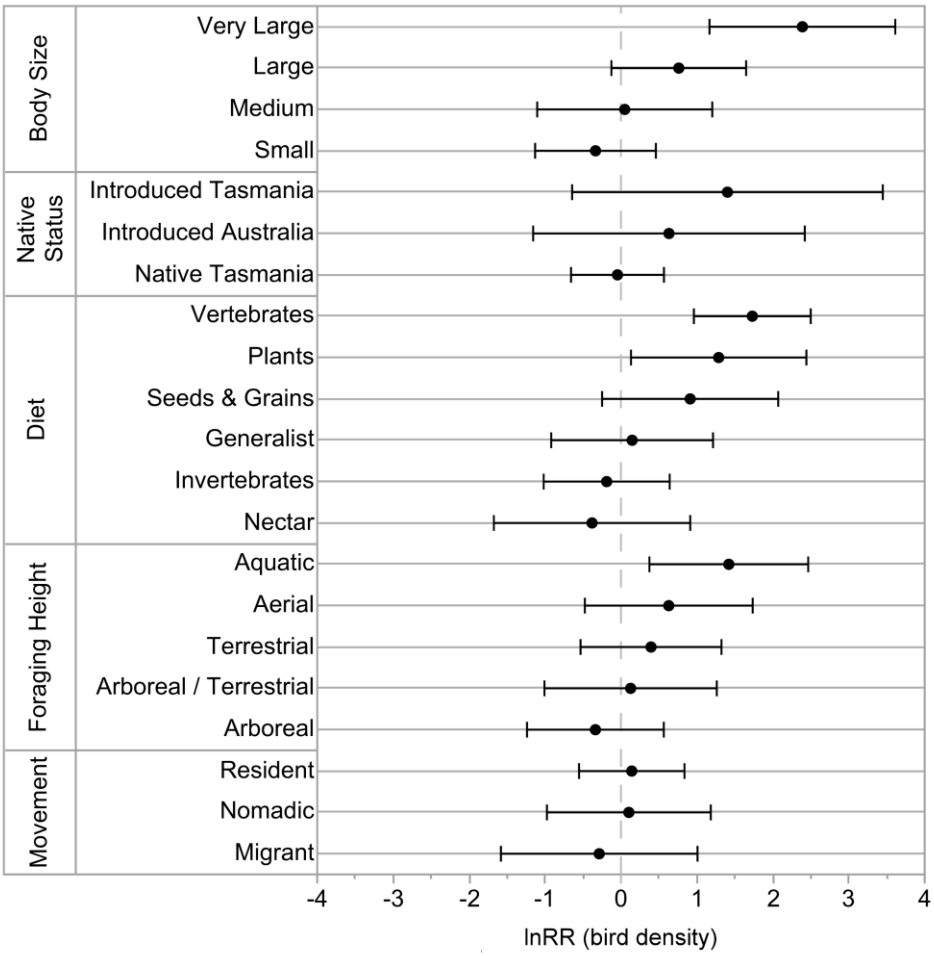


Figure 3.7. Changes in the density of all bird species that shared traits. Positive values of the log response ratio (lnRR) indicate greater abundance in the 2017 survey period. Negative values indicate greater abundance in the 1997 survey period. Error bars are 95% confidence intervals.

Of the 10 species with the lowest response ratios (i.e. less abundant in the recent survey), two are endemic to Tasmania (yellow-throated honeyeater *Lichenostomus flavicollis* and yellow wattlebird *Anthochaera paradoxa*) and 8 are arboreal foragers. The exceptions were eastern rosellas and the yellow-rumped thornbill (*Acanthiza chrysorrhoa*), both of which are classed as ground-foraging species. At historical sites, three species were recorded on transects in the 1997 survey period but were absent in the present survey: masked lapwing (*Vanellus miles*), peregrine falcon and chestnut teal (*Anas castanea*).

Conversely, four species were recorded in the current survey but were previously undetected: satin flycatcher (*Myiagra cyanoleuca*), little corella, long-billed corella and the Pacific black duck (*Anas superciliosa*).

Discussion

The Midlands region of Tasmania is a microcosm of agricultural landscapes elsewhere in Australia and the world, with many of the same threats to avifauna. The well-defined geographical boundaries of the Midlands Biodiversity Hotspot provide an ideal opportunity for studying the impacts of land-use change on birds and other wildlife. We first examined how environmental characteristics influence current patterns of bird species presence and community composition, before considering how this might have changed as a result of agricultural intensification. The composition of bird communities in remnant woodlands of the Midlands was strongly influenced by the amount of surrounding woody vegetation and the elevation of survey sites, but elements of structural complexity such as foliage projective cover (FPC) and leaf litter cover were also important. As in other studies of Australian avifauna, the presence of aggressive noisy miners had strong negative effects on the abundance and richness of small birds (Thomson *et al.* 2015), highlighting what will be a key management challenge for local restoration efforts. Agricultural intensification in the Midlands over the past 20 years appears to have favoured large-bodied birds; populations of some small and medium-sized species, particularly arboreal foragers, could be in decline.

Bird community composition and habitat variables

The greatest gains in avian biodiversity are to be made by restoring habitat in landscapes with low levels of native vegetation cover (Cunningham *et al.* 2014). We found that increasing levels of wooded cover could have significant benefits for native birds in our

study region. Survey sites surrounded by more woodland supported a more diverse bird community with a higher abundance of nectarivores and generalist foragers and fewer exotic species. Four of the seven species with significantly lower abundances in the 2017 survey period (spotted pardalote *Pardalotus punctatus*, crescent honeyeater *Phylidonyris pyrrhopterus*, yellow-throated honeyeater, grey shrike-thrush *Colluricincla harmonica*) were also positively associated with woody vegetation cover. Thus, restoring tree cover might especially benefit these species, which are potential targets for ecological restoration. Species-area relationships have been well described in birds (Villard *et al.* 1999; Heikkinen *et al.* 2004; Watson *et al.* 2005; Smith *et al.* 2011; Ikin *et al.* 2014). Large patches of woodland and landscapes with high vegetation cover provide more resources, such as space, food and safe nesting sites, as well as better access to these resources, and can therefore support larger and more diverse bird populations (Hartley & Hunter 1998; Connor *et al.* 2000; Zanette *et al.* 2000). Increasing vegetation cover might also improve the ability of birds to colonise remnant vegetation, mitigate negative edge effects and encourage settlement by greater numbers of migratory individuals (Murcia 1995; Bélisle *et al.* 2001; Fletcher 2009). Nonetheless, small patches of remnant habitat still contribute to avian biodiversity in fragmented landscapes (Watson *et al.* 2005). This was true for small woodlands and planting sites in the Midlands but only when these habitats were free from high densities of noisy miners.

There was a clear division between bird communities in noisy miner-dominated woodlands, which were mainly comprised of large species characteristic of open-farmland environments (e.g. Australian magpie, laughing kookaburra), and woodlands without miners where smaller species could persist. This pattern is consistent with the earlier survey of the Midlands (MacDonald & Kirkpatrick 2003) and is common to fragmented habitat throughout

Australia wherever aggressive *Manorina* honeyeaters are present (Thomson *et al.* 2015; Kutt *et al.* 2016; O'Loughlin *et al.* 2017). Our study adds that temporal changes in miner density could explain shifts between these two types of bird community. Two woodlands demonstrated large changes in species richness; one increased by 18 bird species and the other declined in richness by the same number. Miner densities at these sites changed from 1.75 to 0.56 miners hectare^{-1} and 0.56 to 1.86 miners hectare^{-1} respectively. Thomson *et al*. (2015) had previously estimated 0.56 miners hectare^{-1} as the threshold above which miners in the Northern Midlands bioregion were expected to negatively affect the occupancy of small birds. Thus, such dramatic changes in community composition are consistent with the impact threshold proposed by Thomson *et al*. (2015); this represents an effective target for the maximum density of noisy miners that could be tolerated by other birds in restored habitats. Methods of controlling miner populations are currently the focus of much scientific inquiry (Davitt *et al.* 2018, but see Recommendations for restoration).

Foliage projective cover and leaf litter cover also had significant effects on community composition. Arboreal foragers and species more typical of wet forests (e.g. satin flycatcher & Tasmanian scrubwren *Sericornis humilis*) were most abundant at sites with high FPC while granivorous species and aerial foragers showed the opposite response. High FPC and leaf litter cover might reflect greater site productivity (FPC was positively correlated with mean annual rainfall) and a more abundant and diverse prey-base for insectivorous birds (Taylor 2008; Montague-Drake *et al.* 2009; Watson 2011). Certainly, all three species of robin included in our analysis showed positive associations with leaf litter cover. Sites with high FPC might also provide better opportunities for nesting sites and greater protection to birds from introduced predators like feral cats (McGregor *et al.* 2015). Birds that were negatively associated with leaf litter cover tended to be more common in

degraded woodlands where pasture grasses were the dominant groundcover (e.g. forest raven & common starling).

Elevation had a strong influence on community composition but only one species, the grey fantail, was found to contribute significantly to this effect. The apparent negative relationship between grey fantails and elevation could be the result of seasonal migratory behaviour in this species, which is poorly understood in Tasmania (Ford 1981). Some birds, such as the crescent honeyeater, are known to migrate altitudinally in response to changes in food availability but individual trends for these elevational migrants could have been masked in our analysis because we combined survey data from different seasons. Given that our study sites were mainly restricted to the rift valley of the Midlands, our surveys were not designed to reveal the full effects of elevation on Tasmanian bird assemblages. Nonetheless, our models showed that endemics like the black currawong, black-headed honeyeater and yellow-throated honeyeater were more common at higher altitudes.

Traits and changes in abundance

The bird community of Tasmania is distinct from those of mainland Australia but is also relatively depauperate (MacDonald & Kirkpatrick 2003). This could result from a dispersal filter to the island or Tasmania's climatic suitability. Of the terrestrial bird species that settled in Tasmania, and when compared to those of mainland Australia, few have been recognised as of 'conservation concern', 'decliners' or as sensitive to the area of woodland remnants (Watson 2011; Ikin *et al.* 2014; Lindenmayer *et al.* 2018). For example, of the 26 species of declining woodland bird analysed by Watson (2011), only the dusky woodswallow (*Artamus cyanopterus*) and swift parrot (*Lathamus discolor*) are present in Tasmania. This could reflect the paucity of research on woodland birds in Tasmania – species of

conservation concern are yet to be identified – or might otherwise indicate that local species are more resilient to the impacts of land-use change and are not at overall risk.

Of the 51 species that we examined, seven showed significantly lower current densities than in the 1997 survey period, but without data collected from the intervening years, we cannot be certain if these differences truly reflect population declines. This is particularly so for striated pardalotes (*Pardalotus striatus*) and crescent honeyeaters, both of which have strong migratory patterns that could be influenced by yearly variations in climate. Many of those species with lower abundances share a small to medium body size and are arboreal foragers. Birds with these life-history traits may be particularly sensitive to continued habitat loss and the degradation of structural complexity in remnant woodlands, for example by livestock grazing or domestic firewood collection. Consistent with our findings, the spotted pardalote, striated pardalote, grey shrike-thrush and yellow rumped-thornbill have been identified as in regional decline elsewhere in Australia, although the reasons for their decline remain unclear (Watson *et al.* 2005; Radford & Bennett 2007; Lindenmayer *et al.* 2018). Unlike Lindenmayer *et al*. (2018) who found declines in numbers of large-bodied birds, we found an increase in larger species.

The diversification of farms in the Midlands from sheep grazing to cropping has favoured large-bodied granivorous birds, namely *Cacatuids*, by providing these species with a rapidly expanding food source. The proliferation of farm dams and conversion of pastures has also benefitted another large but mainly herbivorous species, the Australian shelduck. Incidental to our bird surveys, we recorded flocks of 189 sulphur-crested cockatoos and 291 shelducks foraging in pastures adjacent to our field sites. Corellas were absent in the 1997 survey period but were frequently recorded in the present study (MacDonald 2001). The

first formal record of little corellas in Tasmania was in 1983 on a farm in the Northern Midlands that is now the focus of landscape restoration (Green 1984). We expect that corellas will continue to increase their abundance and distribution in much the same way as the laughing kookaburra following its introduction to the Midlands in 1906 (Higgins 1999).

Populations of raptors and other large carnivorous species like the forest raven may have also increased. This could be because of a greater availability of animal carcasses following the functional loss of the native apex-predator, the Tasmanian devil (Cunningham *et al.* 2018), higher stocking rates of lambs, reduced persecution and use of poisons by landowners, or perhaps even habitat fragmentation itself. Aerial foragers, which were mostly raptors, showed a preference for the habitat edge and landcover diversity at survey sites, possibly reflecting their hunting strategies.

We found a high proportional increase in species that are typically associated with wetlands. Record rainfall meant that in 2016 many of the ephemeral lagoons near to our survey sites were filled and some paddocks were flooded (BOM 2018). This attracted dispersive species of duck, white-faced herons and other migratory birds like the swamp harrier, such that they were more frequently recorded within neighbouring woodlands. In contrast, the historical survey period was undertaken at the beginning of Australia's Millennium Drought. Wetland birds could also have benefitted from the widespread creation of farm dams to support crop irrigation.

Recommendations for restoration

The invasion of restored habitat by noisy miners poses significant risk to the avian biodiversity objectives of landscape restoration in the Midlands. The habitat preferences of noisy miners are well established: eucalypt-dominated woodlands of high productivity

(Montague-Drake *et al.* 2011), a high perimeter-area ratio (Clarke & Oldland 2007; Maron *et al.* 2013) and low structural complexity (Maron *et al.* 2013; Robertson *et al.* 2013; Thomson *et al.* 2015). Therefore, to abate the threat of miners, restoration managers should maximise levels of shrub cover (Robertson *et al.* 2013), establish mixed stands of eucalypt and non-eucalypt tree species (e.g. *Bursaria* spp., Hastings & Beattie 2006) and plant in blocks rather than corridors whenever that is feasible (Clarke & Oldland 2007; Taylor *et al.* 2008). Clarke and Oldland (2007) investigated penetration by noisy miners of remnant woodlands in Victoria. They suggest that for woodlands to be miner-free, they must be larger than 36 ha in size and linear vegetation must be greater than 600 m wide. The composition of plantings would, however, also determine the size and length of planting sites necessary to avoid domination by noisy miners.

We also encourage restoration managers to trial novel planting configurations and test for the most 'miner-resilient' formations. This could include plantings that are bordered by tree species, native or exotic, that have a very dense foliage (Marzluff & Ewing 2001). Alternatively, eucalypt plantings could have higher than natural stem densities at the edge but retain an open structure within their interior. Some landowners in the Midlands regularly clear vegetation along fence lines to avoid damage by tree falls. The associated soil disturbance has led to dense resprouting of *Acacia* trees (Spooner 2005) around the perimeter of woodland remnants and may function to prevent colonisation by noisy miners. Small islands of dense vegetation could also be dispersed within miner-dominated remnants to facilitate the movement of small birds through revegetation corridors, analogous to paddock trees as stepping stones for birds across the agricultural matrix (Fischer & Lindenmayer 2002).

Miner culls have also been proposed as a management action to encourage the return of small birds to remnant habitat (Major *et al.* 2001; Maron *et al.* 2013). Some authors have reported immediate benefits of culling miners (Grey *et al.* 1997; Debus 2008), but more recent studies have found no short-term effects on bird species richness and abundance (O'Loughlin *et al.* 2017; Davitt *et al.* 2018). The ecological benefit of culls probably depends on the initial density of miner birds in degraded habitat (Crates *et al.* 2018; Davitt *et al.* 2018). Further research is needed to test whether culls are more successful in remnant woodlands that are contiguous with revegetation sites or when there is a combined habitat restoration effort (Debus 2008).

In one small woodland remnant, the establishment of a neighbouring eucalypt plantation led to a doubling of native bird species richness. This suggests that even when revegetation is not designed with the purpose of improving biodiversity, increasing levels of woody vegetation cover can still benefit local avifauna. It is unclear, however, whether this increase in species richness was due to the provision of more habitat, improved connectivity with nearby remnants or the associated decline in noisy miner abundance. Forestry plantations could be incorporated into the design of landscape restoration. Law *et al*. (2014) found that as eucalypt plantations in a farmland mosaic of northern New South Wales matured, abundance of noisy miners declined. Productive eucalypt plantations enhance the biodiversity value of the matrix between remnants (Huth & Possingham 2011) and can provide suitable foraging habitat for some Australian birds (Hobbs *et al.* 2003; Kavanagh *et al.* 2007; Law *et al.* 2014).

Even though many of our small woodland sites were degraded and had become dominated by noisy miners, their conservation value should not be ignored. Huth and

Possingham (2011) showed that there is greater benefit to avian biodiversity in restoring the structural complexity of vegetation in small and degraded woodlands than there is in increasing their size. Moreover, connecting small remnants without first restoring structural complexity might only lead to the creation of more habitat for miners (Major *et al.* 2001). Small remnants could be improved by reducing grazing pressure from livestock or perhaps through ecological burns such that leaf litter cover and FPC are restored. Gorse shrubs are present in many woodland remnants in the Midlands and are often the only feature that provides vertical structural complexity in this habitat. As has been suggested for *Tamarix*, a genus of invasive weeds in North America, gorse should be replaced gradually by native shrubs that offer comparable vegetation cover, rather than being immediately cleared (Sogge *et al.* 2008). Gorse shrubs within remnants provide small birds with safe nesting sites as well as protection from noisy miners and other predators (Chapters Four and Five). We also recorded a range of species using gorse invaded pastures to travel between woodland remnants, highlighting the weeds value in softening the agricultural matrix.

Large increases in the abundance of hollow-nesting birds, including sulphur-crested cockatoos, common starlings, galahs and corellas, has likely increased competition for what was an already limited resource in the Midlands. Competition for breeding hollows is thought to contribute to declining numbers of eastern rosellas in Tasmania (Koch *et al.* 2008b) and could increasingly threaten other species like the dusky woodswallow. Tree hollows suitable for breeding birds can take more than 100 years to form in *Eucalyptus* (Koch *et al.* 2008a) and so revegetation sites will not be able to relieve such demand in the immediate future. Artificial nest boxes could be used to supplement natural tree hollows within remnant woodlands but are unlikely to attract hollow breeding birds to young stands of vegetation (Le Roux *et al.* 2016).

Conclusion

Agricultural intensification in the Tasmanian Midlands appears to have benefitted some bird species. These tended to be larger birds with either a granivorous or carnivorous diet. In contrast, arboreal foragers and nectarivores that prefer areas of high woodland cover and rely on more complex vegetation structure could be in decline. A continued long-term monitoring effort is necessary to confirm changes in bird abundance because our analysis was limited to comparisons between just two survey periods. This is especially urgent considering the emerging trend of population decline in common birds around the world (Inger *et al.* 2015; Lindenmayer *et al.* 2018; Stanton *et al.* 2018), the rapidly changing environment in the Midlands, and the poor representation of Tasmanian species in Australian bird data. In a landscape like the Midlands, which has very little remaining native vegetation, simply increasing levels of wooded cover will have significant benefits for local bird populations (Radford *et al.* 2005). To maximise the conservation value of restoration efforts, however, competition between birds and the specific habitat preferences of individual species must also be addressed.

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Chapter Four

Chronic stress in superb fairy-wrens occupying remnant woodlands: are noisy miners to blame?

"Greenhill", a noisy miner-dominated woodland with an understorey of bracken fern.

Abstract

Interactions between competing species may be intensified when they are restricted to small patches of remnant habitat, potentially increasing physiological stress in individuals. The effects of interspecific competition on stress in wildlife remain largely unexplored. In Australia, remnant woodlands are often dominated by aggressive honeyeaters, especially the noisy miner (*Manorina melanocephala*). Harassment of smaller birds by miners may result in their exclusion from suitable woodland habitat. We tested whether the presence of noisy miners is also associated with elevated stress in a model species of small passerine bird, the superb fairy-wren (*Malurus cyaneus*). We sampled fairy-wrens from six sites, three remnant woodlands with noisy miners and three larger fragments of reserved habitat without noisy miners. Differential white blood cell counts were used to infer levels of chronic stress. We also assessed variation in body condition and the prevalence of blood parasites (*Haemoproteus* spp.) to test for associations between stress and parasitemia. The mean heterophil-to-lymphocyte (H:L) ratio was 1.8 × higher among superb fairy-wrens living in miner-dominated woodlands, suggesting higher levels of chronic stress. Individuals with higher stress appeared to be in poorer condition, as indicated by fat scores and residual body mass. Prevalence of blood parasites was generally high and was highest in reserved habitat (59%) where miners were absent. Birds with blood parasites living in these habitats had higher H:L ratios than birds without blood parasites but the intensity of infection and H:L ratio was inversely related. Our results suggest that birds persisting in the presence of noisy miners might experience chronic stress, but further study is necessary to separate the relative importance of noisy miner aggression from other potential stressors in small patches of degraded woodland. Stress induced by interspecific aggression should be considered in future studies of wildlife living in remnant vegetation.

Introduction

When an animal is faced with conspecific or heterospecific aggression, the acute stress response can facilitate a quick escape to refuge or aggressive confrontation by activating the sympathetic nervous system and promoting the mobilisation of energy stores (Romero & Wingfield 2016). However, where such encounters are frequent or the perceived threat of conflict is prolonged, the stress response can become maladaptive. Stressful stimuli trigger a neuroendocrine cascade that culminates in the release of glucocorticoid hormones (e.g. corticosterone) from the adrenal cortex (Sapolsky *et al.* 2000). Sustained elevation of these hormones can radically disrupt an animal's behavioural and physiological state and is generally described as chronic stress. Chronic stress can reduce reproductive success (Silverin 1986; Ellenberg *et al.* 2007; Beldade *et al.* 2017), immunocompetency (Hing *et al.* 2016), growth (Suorsa *et al.* 2004) and survival (Ethan Pride 2005; Koren *et al.* 2012). Understanding the challenges that cause chronic stress in wildlife is therefore essential to mitigating such detrimental fitness consequences, and thereby improve conservation outcomes.

Fear is a source of stress for many species and is most simply understood in the context of predator-prey interactions (Clinchy *et al.* 2013). Individuals of prey species might experience chronic stress because of repeated and unpredictable attacks by predators, or as a result of observing such attacks on conspecifics. Indeed, witnessing a very brief simulated predator attack was sufficient to elicit a glucocorticoid response in European starlings (*Sturnus vulgaris*, Jones *et al.* 2016). Prey animals living in risky environments might also increase anti-predator behaviours (e.g. vigilance) at the cost of reduced foraging efficiency or trade off the most valuable foraging patch for one that provides greater levels of cover from predators (Brown 1988; Verdolin 2006). Thus, the psychological effects of predation

risk alone have the potential to restrict access to food and lead to chronic stress or 'allostatic overload', defined as the state in which the cumulative daily energy requirements of an animal exceed the amount of energy available in the environment (McEwen & Wingfield 2003). Aggressive competition over resources like food, space and mates can cause stress in similar ways to encounters between predators and prey (Creel *et al.* 2013). In territorial species and those with social hierarchies, persistent competition can cause chronic stress in both dominant (Creel 2005; Gesquiere *et al.* 2011) and subordinate individuals (Gilmour *et al.* 2005). As with the effects of predators, competition could also induce chronic stress indirectly, by making it more difficult for individuals of low status to acquire essential resources like food and shelter. Most studies of competition and stress, however, have been within species (but see Narayan *et al.* 2015; Santicchia *et al.* 2018), despite interspecific competition having the same or greater potential for overt aggression (Danley 2011; Lailvaux *et al.* 2012; Grether *et al.* 2013).

Stress from competition could be amplified among wildlife that are restricted to small fragments of habitat because of changes in resource availability and distribution that intensify agonistic interactions between species (Didham *et al.* 2007). At the same time, animals living in small patches might be limited in their ability to seek refuge from aggression by competitors because vegetative cover is often degraded by edge effects (caused for example by invasion of weeds or livestock grazing, Murcia 1995). Other stressors might also be amplified in small fragments. Socially-mediated stress can be increased because of changes in population density or group sizes (Creel *et al.* 2013; Gabriel *et al.* 2018), the activity or abundance of predators might be higher (Clinchy *et al.* 2011), food availability may be reduced (Hinam & Clair 2008; Chapman *et al.* 2015) or animals could be without shelter from the elements (Wingfield & Ramenofsky 2011).

In Australian woodlands, a hyperaggressive honeyeater, the noisy miner (*Manorina melanocephala*), has a broadly negative impact on the composition of bird communities (Thomson *et al.* 2015). Miners form colonies that exclude smaller bodied birds (< 60 g) from suitable habitat and are frequently implicated in the decline of Australian avifauna (Piper & Catterall 2003; Maron *et al.* 2013; Mortelliti *et al.* 2016). They have benefitted from habitat fragmentation and often dominate remnant woodlands with high edge-to-area ratios and an open or degraded midstory (Clarke & Oldland 2007; Thomson *et al.* 2015). Ellis *et al.* (2011) suggested that interference competition with miners has the potential to trigger a stress response in small woodland birds. This presents one mechanism by which noisy miners could exclude other species. Chronic stress could either compel other birds to leave areas colonised by miners or reduce individual fitness in those birds that persist, for example by reducing foraging efficiency or increasing vulnerability to pathogens (Gervasi *et al.* 2016). Miner presence is also positively associated with the abundance of other large-bodied predatory birds (Thomson *et al.* 2015), which could further escalate levels of stress among small species living in the presence of miners.

We compared levels of chronic stress in individuals of a small passerine, the superb fairy-wren (*Malurus cyaneus*), occupying remnant habitat where noisy miners were common, with those living in larger reference woodlands without noisy miners. We chose the superb fairy-wren as our model species because fairy-wrens are among the last birds to be excluded from woodlands by miners and can still be found cohabiting with them in some locations. Fairy-wrens were, therefore, also expected to represent the best-case stress scenario for other species of the woodland bird community. We used differential white blood cell counts to infer levels of stress. The heterophil-to-lymphocyte (H:L) ratio is a reliable measure used to compare levels of chronic stress in birds (reviewed by Davis *et al.*

2008; Goessling *et al.* 2015; Davis *et al.* 2018). In stressful situations, the secretion of glucocorticoids by the hypothalamic-pituitary-adrenal axis up-regulates the production of heterophils and lowers the number of circulating lymphocytes (Sapolsky *et al.* 2000). Thus, higher H:L ratios indicate comparatively higher levels of stress. The H:L ratio integrates levels of stress over longer periods of time than do measures of hormone concentrations, providing greater opportunity to measure stress without exaggeration due to the stress of capture and blood sampling itself (Cīrule *et al.* 2011; Goessling *et al.* 2015).

Methods

Study sites

The Tasmanian Midlands lies in the floor of a north-south rift valley. More than 200 years of agriculture in this region has led to fragments of temperate woodland surrounded by cropping and pastures, with < 10% of native eucalypt woodlands remaining (Jones & Davidson 2016). This fragmentation has favoured the noisy miner (*M. m. leachi*), such that many remnant woodlands are now dominated by this species (MacDonald & Kirkpatrick 2003). We captured fairy-wrens in six study sites across the Midlands; all were fragments of the original woodland vegetation. Three of these were small remnant woodlands on farmland, hereafter referred to as *remnants*, and three were larger fragments of reserved woodland, hereafter referred to as *reserves*.

Remnants ranged from 32-72 hectares in size and were occupied by noisy miners (Greenhill: 41°52’15”S, 147°18’02”E, Tervue: 42°16’24”S, 147°39’52”E, Lewisham: 41°59’12”S, 147°29’57”E). Vegetation in remnants comprised three dominant eucalypt tree species (*Eucalyptus amygdalina*, *E. pauciflora* and *E. viminalis*) and a patchy understory of pasture grasses, bracken (*Pteridium esculentum*), rushes (*Juncus* spp.), spiny-head mat-rush

(*Lomandra longifolia*) and exotic weeds like gorse (*Ulex europaeus*). Remnants were isolated by pasture on all sides. Mean densities of noisy miners in remnants were estimated by counting birds along an 800 × 100 metre transect on six separate occasions (Chapter Three). These were 0.43 miners ha^{-1} at Tervue, 2.02 miners ha^{-1} at Lewisham and 3.47 miners ha^{-1} at Greenhill. The same was done for reserves but no noisy miners were ever observed over two years of bird surveys and associated fiedwork.

Reserves, were all > 1,000 hectares and included two sites in Nature Reserves (Powranna: 41°41'34"S, 147°13'58"E, Tom Gibson Reserve: 41°46'30"S, 147°18'14"E) and one within a large Conservation Area (Gravelly Ridge: 42°32'42"S, 147°27'29"E). Vegetation in these reserves included two dominant tree species (*Eucalyptus amygdalina* and *E. tenuiramis*) and a more complex midstory than in the remnants, with low branching trees including wattles (*Acacia dealbata*), sheoaks (*Allocasuarina littoralis*), native cherry (*Exocarpos cupressiformis*) and bottlebrushes (*Callistemon pallidus*). The understory was comprised of similar species to remnants but with an absence of weeds and a greater diversity of herbaceous groundcover.

Study species

Superb fairy-wrens are small, sexually dichromatic passerines that are common in south-eastern Australia. The larger (9-13 g at our study sites), darker, nominate subspecies (*M. c. cyaneus*) is found throughout Tasmania. Superb fairy-wrens are insectivorous and sedentary, living in family groups that defend territories year-round (Rowley 1965). Territories range in size from 0.83 to 8.6 ha dependent upon habitat quality (Nias 1984; Chan & Augusteyn 2003). Fairy-wrens were observed breeding from the beginning of September through to February. At remnant sites, fairy-wrens were frequently seen being

chased and dived upon by noisy miners and occasionally other avian predators, including grey butcherbirds (*Cracticus torquatus*), the introduced laughing kookaburra (*Dacelo novaeguineae*) and species of raptors (e.g. brown goshawk *Accipiter fasciatus*).

Measures of condition and chronic stress

Throughout winter and spring of 2017 (July-November), a total of 86 adult superb fairy-wrens were captured using mist nets, 42 from remnant woodlands and 44 from reserves. Birds were sampled alternately from reserves and remnants to avoid seasonal bias between treatments and to account for any differences in stress levels over time. Each individual was colour banded for identification and the following was noted: sex, moult stage if male (% nuptial plumage), number of pin feathers, tarsus and head-plus-bill length (0.01 mm), wing and tail length (nearest mm), body weight using a digital scale (0.01 g), and a score of fat stored in the bird's furculum (scale 0-5, Helms & Drury 1960). Residual body mass was determined from a regression of weight on tarsus length. Within 10 minutes of capture, each bird was blood sampled (< 75 µl) by brachial venipuncture using a 26-guage needle and drawing blood into a heparinised microcapillary tube. Previous studies in other small passerines have shown that H:L ratios are only affected by handling stress between 30 minutes and one hour after capture (Davis 2005; Cīrule *et al.* 2011).

The wedge method (Houwen 2002) was used to make up to three blood smears per individual on glass slides. Smears were air-dried, fixed in methanol for 15 minutes and stained using May-Grünwald and Giemsa stains for a further 15 minutes each. Remaining blood was spun in a microhaematocrit centrifuge for four minutes. Packed cell volume (PCV) was measured as the length of the capillary tube containing packed cells (nearest mm) divided by the total blood column length. Slides were examined by a single observer at

×1000 magnification under oil immersion, beginning at the feathered edge of each smear and continuing until 100 leukocytes were counted and the heterophil-to-lymphocyte ratio could be determined. Lysed leukocytes were not included in the counts. Each slide was examined blind as to the location where the bird was captured. Five randomly selected slides were counted again to obtain an estimate of repeatability, which was high (r = 0.98, n = 5). Apart from leukocytes, the number of polychromatic erythrocytes, anucleated erythrocytes, thrombocytes and blood parasites that were present in each field of view (FOV) was also recorded. The number of parasites observed for every 10,000 erythrocytes was calculated to assess the intensity of parasite loads. An estimate of the number of erythrocytes per FOV was first produced by counting a representative monolayer across each of 10 fields. Parasite intensity was equal to the total number of infected erythrocytes divided by the product of FOVs scored and the mean number of erythrocytes per FOV.

Data analysis

We used generalised linear models in R (R Development Core Team 2017) with a Gaussian distribution and identity link to assess the effect of *Fragment Type* (remnant/reserve) on H:L ratio in fairy-wrens. We included combinations of three additional variables that have previously been shown to influence H:L ratio in birds as covariates: *Sex*, *Parasite presence* (presence/absence) and *Time* of capture (am/pm). The presence of noisy miners meant that it was inherently difficult to find study sites with both miners and fairy-wrens and also that there were many fewer individual fairy-wrens living in these populations. Consequently, we did not include *Site* as a random effect in our models because fairy-wrens were sampled from only three replicate patches of habitat for each level of fragment type; variance estimates are imprecise when there are fewer than five levels of a random variable (Harrison *et al.* 2018). We substituted site for the fixed effect of

fragment type but found that the latter was a better predictor and so only report the results of fragment type models. We used multi-model inference and an information theoretic approach (Akaike's Information Criterion, AIC*c*) to rank models (Burnham & Anderson 2002). Those with AIC*c* values within 7 units of the model with lowest AIC*c* were included in the final candidate set (Burnham *et al.* 2010).

We analysed birds captured in winter and spring separately. This was primarily because fewer birds were sampled in winter (n = 25) and they came from only two sites (Tom Gibson reserve and Lewisham remnant), but also to avoid comparing H:L ratios of birds that were potentially in different life-history stages. Ten birds were first captured in winter and later recaptured in spring; for these birds we used the relevant H:L ratio in the analysis of each season. To compare the condition of fairy-wrens between fragment types, we again used generalised linear models (Gaussian with identity link), replacing H:L ratio with PCV and residual mass as the response variables. We calculated correlations of condition indices for all birds (winter and spring captures) using the *hetcor* function in the *polycor* package of R (Fox 2016). In all tests, we $\log_{10}$-transformed H:L ratio and parasite intensity to improve the normality of residuals. Mean ± standard error are reported.

Results

Across all smears, 72 ± 2% of cells were lymphocytes and 26 ± 2% were heterophils. Fairy-wrens living in remnant woodlands had higher H:L ratios than birds living in reserves (0.60 ± 0.11 *versus* 0.33 ± 0.04 respectively). Within remnants, H:L ratios were highest at the site with the greatest abundance of noisy miners, Greenhill, followed by Lewisham and then Tervue where densities of noisy miners were low (Fig. 4.1). The final candidate set of models that described factors influencing H:L ratio contained five models for spring and five models

for winter (Δ AIC*c* < 7 units). For spring, the top three models carried 44%, 26% and 15% of the weight, respectively. The top model included the additive effects of fragment type, parasite presence, sex and time. Birds in remnants had H:L ratios 0.24 units higher than those in reserves, and H:L ratio increased by 0.17 units when birds had parasites than not. Males had 0.1 higher H:L ratios than females and H:L ratios decreased with time (Table 4.1).

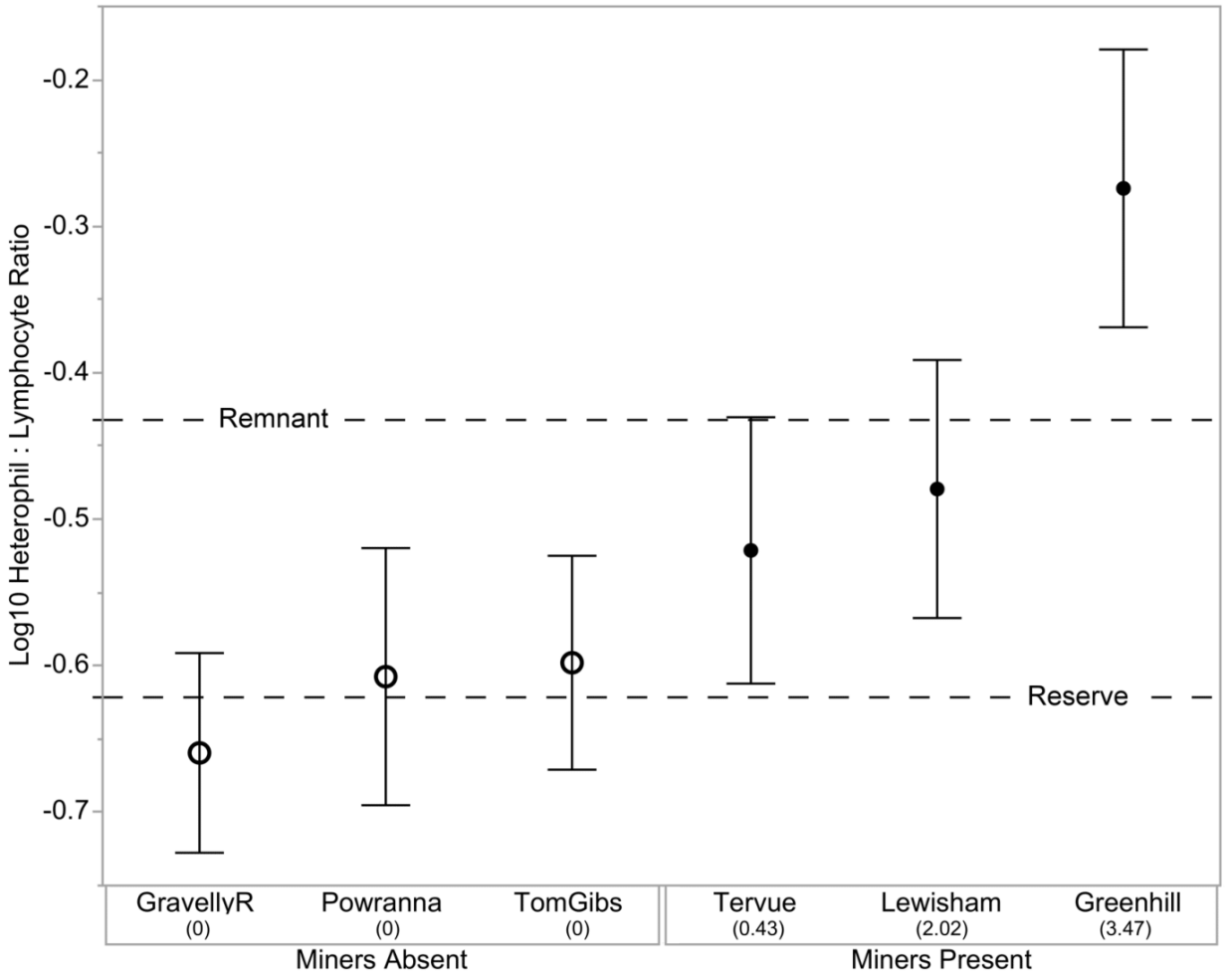

Figure 4.1. The heterophil : lymphocyte ratio (H:L log_{10}-transformed) was higher among superb fairy-wrens occupying remnant woodlands (closed circles) than in fairy-wrens occupying nature reserves (open circles). The density of noisy miners at each site is specified in parentheses (miners ha^{-1}). Data points specify the mean H:L ratio for birds captured in spring (*n*=71) and error bars represent standard error. Dashed lines are the mean H:L ratio for reserve and remnant birds.

Table 4.1. Regression analysis of the relationship between stress (heterophil:lymphocyte ratio log_{10}-transformed) in superb fairy-wrens sampled in spring (n=71) and fragment type (remnant or *reserve*), parasite presence (present or *absent*), sex (male or *female*), and the time of capture (*am* or pm). Parameter estimates ± se for factors are differences compared to the reference level in italics above and models are ranked by AIC*c*. See Appendix B.1 for models of H:L ratio in fairy-wrens captured in winter (n = 25) and spring models with W < 0.10.

Spring Models								
AIC*c*	Δ AIC*c*	*W*	Adj. R^2	Fragment Type	Parasite Prevalence	Fragment Type × Parasite Pres.	Sex	Time
27.25	0.00	0.44	0.17	0.237±0.069	0.167±0.069	-	0.114±0.066	-0.149±0.095
28.33	1.09	0.26	0.13	0.234±0.071	0.152±0.071	-	-	-
29.41	2.16	0.15	0.17	0.271±0.095	0.202±0.097	-0.076±0.143	0.118±0.067	-0.138±0.097

The second-best model was a subset of the parameters included in the top model while the third model included an interaction between fragment type and parasite presence (Table 4.1). This interaction reflects the higher prevalence of parasites among birds in reserves and the higher H:L ratios in infected individuals (see below) even though overall birds in remnants had higher H:L ratios. Model fit for birds captured in winter was very low because of a much smaller sample size but the direction of main effects was the same as for spring. The top model in winter included just fragment type with H:L ratios 0.15 units higher in remnants than in reserves (Appendix B.1). The second model also included parasite presence with H:L ratios increasing by 0.13 units when parasites were present. Subsequent models also included sex and time, but these carried 10% or less model weight.

H:L ratio was negatively correlated with the residual mass and fat score of birds but was unrelated to PCV (Table 4.2). None of our measures of individual condition appeared related to whether the bird sampled was from a remnant or reserve (Table 4.3), but residual mass was significantly lower for those birds captured in winter (0.17 ± 0.10 *versus* -0.49 ± 0.14, t_{49}=-3.79, p=< 0.05). There was no systematic difference in H:L ratio for the 10 birds first captured in winter and later recaptured in spring (paired t-test, t_9=2.26, p=0.72).

Table 4.2. Pairwise correlation matrix between measures of individual condition in superb fairy-wrens.

	Log_{10} H:L Ratio	Residual Mass	Packed Cell Volume	Log_{10} Parasite Intensity	Parasite Presence	Fat Score
Log_{10} H:L Ratio	1	-0.22 (0.10) p=0.046	0.12 (0.11) p=0.261	-0.33 (0.15) p=0.045	0.09 (0.14)	-0.30 (0.11)
Residual Mass	n=85	1	0.15 (0.11) p=0.168	-0.00 (0.17) p=0.979	0.18 (0.14)	0.41 (0.09)
Packed Cell Volume	n=84	n=84	1	0.21 (0.16) p=0.220	-0.07 (0.14)	0.25 (0.11)
Log_{10} Parasite Intensity	n=37	n=36	n=37	1	-	-0.05 (0.18)
Parasite Presence	n=86	n=85	n=84	-	1	0.13 (0.14)
Fat Score	n=86	n=86	n=85	n=37	n=86	1

Standard errors are given in parentheses, *n*-values are the number of observations for each correlation. For correlations between continuous variables, Pearson's correlation coefficients are given with *p*-values indicating the significance of the relationship. Correlations between parasite presence or fat score and continuous variables are polyserial, fat score by parasite presence is polychoric. Significance of polyserial and polychoric correlations was not assessed.

Table 4.3. Regression analysis of the relationship between the condition of superb fairy-wrens and fragment type (remnant/*reserve*), parasite presence (present/*absent*), sex (male/*female*), time of capture (*am*/pm) and season (*spring*/winter). Parameter estimates ± se for factors are differences compared to the reference level in italics above. See Appendix B.2 for models with $W < 0.10$.

Response Variable	AIC*c*	Δ AIC*c*	*W*	Adj.R^2	Fragment Type	Parasite Presence	Sex	Time	Season
Residual Mass	226.89	0.00	0.95	0.19	-	0.213±0.168	-	-	-0.575±0.186
PCV	647.66	0.00	0.44	0.04	2.363±1.589	-	-	-	-3.478±1.839
	649.10	1.44	0.21	0.01	2.495±1.610	-	-	-	-
	649.56	1.90	0.17	0.01	-	1.001±1.696	-	-	-3.896±1.924

Haemoproteus was the only blood parasite recorded. Of 86 birds examined, 37 (43%) were infected by *Haemoproteus*. Among these birds, the intensity of infection ranged from 0.24-195 infected cells per 10,000 erythrocytes (31 ± 6.69 infected cells). The prevalence of *Haemoproteus* was higher in birds from reserves than from remnants (59% *versus* 26% respectively, $p = 0.003$ Fisher's exact test) and parasites were recorded at all but one remnant site (Tervue). Infected birds had higher H:L ratios (0.37 ± 0.04 *versus* 0.27 ± 0.06) in reserves but not in remnants (Fig. 4.2a). The interacting effect of fragment type and parasite presence was included in the third best model of H:L ratios in spring. Of those birds with blood parasites, the intensity of infection was negatively correlated with H:L ratio ($F_{1,35} = 4.38$, $p = 0.043$, $r = -0.33$). To investigate this pattern further, we first partitioned birds by fragment type and the relationship remained significant in reserves (Fig. 4.2b, $F_{1,24} = 5.54$, $p = 0.027$) but was not evident in remnants ($F_{1,9} = 0.02$, $p = 0.90$). To determine whether this was the result of an increase in lymphocytes or decrease in heterophils we then plotted the intensity of infection against the number of each cell type separately. Lymphocytes increased with the number of infected cells in birds ($F_{1,36} = 5.02$, $p = 0.031$) but this result

was influenced by one bird with a very high parasite load (Fig. 4.2c). Heterophil concentration was unrelated to parasite intensity. Neither the presence nor intensity of parasites was related to PCV, furcular fat, residual mass or the sex of individuals (Table 4.2).

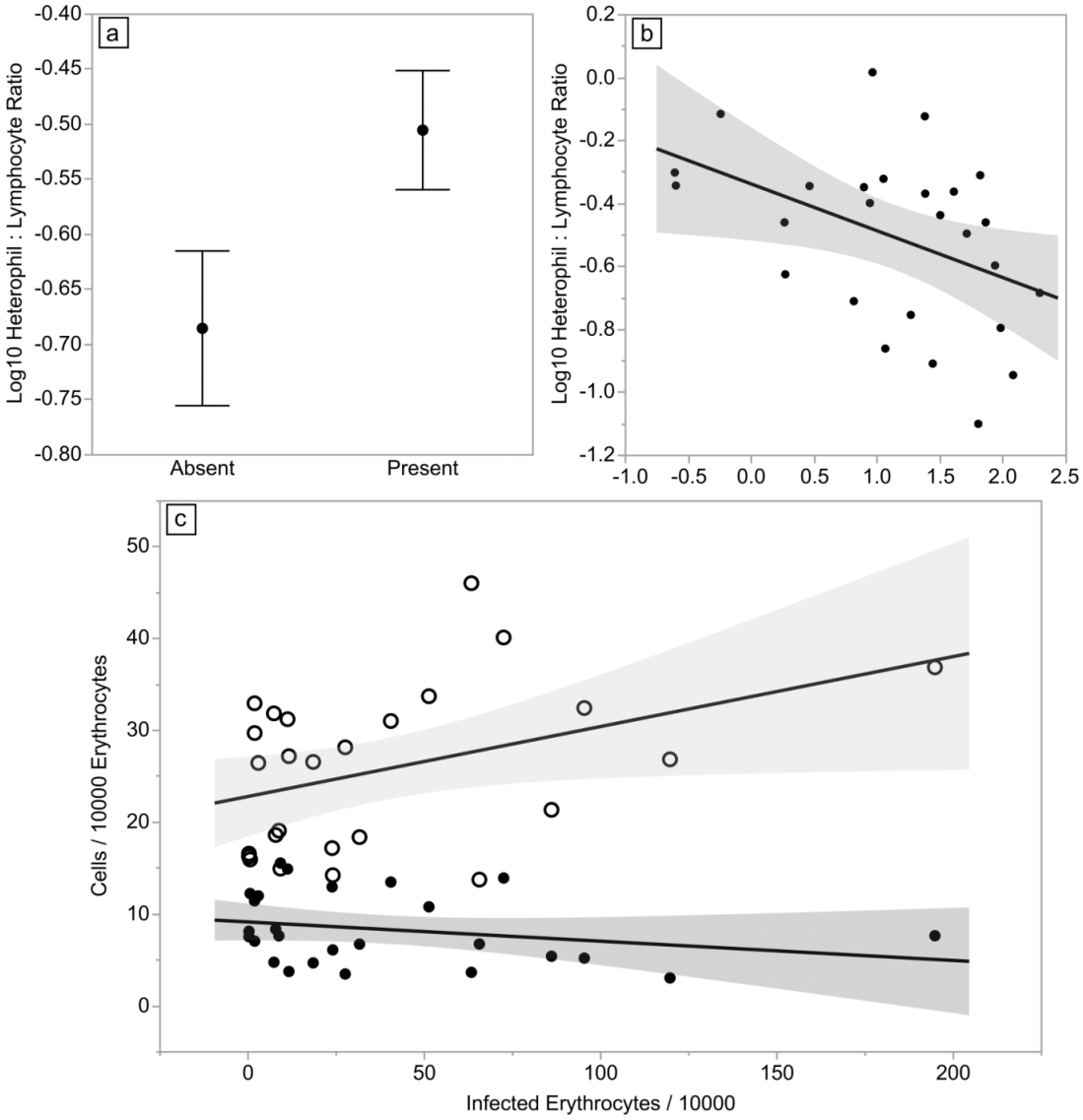

Figure 4.2. The relationship between heterophil:lymphocyte ratio and parasitemia of *Haemoproteus* in superb fairy-wrens. Shown are (**a**) the mean H:L ratio of fairy-wrens living in nature reserves when parasites were present (n = 26) and absent (n = 18) with standard error bars, (**b**) a regression of parasite intensity (log_{10}-transformed) against H:L ratio for those birds that were infected (Adj. R^2 = 0.15, t_{24} = -2.35, p = 0.03) and (**c**) regressions of the number of lymphocytes (open circles, Adj. R^2 = 0.10, t_{37} = 2.24, p = 0.03) and heterophils (closed circles, Adj. R^2 = 0.02, t_{37} = -1.26, p = 0.22) in birds with parasites against parasite intensity. Shaded areas indicate 95% confidence intervals of the fitted lines.

Discussion

Consistent with our prediction, the mean heterophil-to-lymphocyte (H:L) ratio of superb fairy-wrens occupying remnant woodlands on farms was 1.8 × higher than for conspecifics in reserves, suggesting that remnant woodlands present a more stressful living environment. Identifying the proximate factor causing this stress remains difficult because multiple stressors are potentially correlated in small patches of remnant habitat. Nevertheless, in the fragmented woodlands of eastern Australia, miner species (genus *Manorina*) are the most influential factor on the distribution, abundance and diversity of small birds, and the effect of noisy miners is estimated to be strongest in the Midlands of Tasmania (Thomson *et al.* 2015). Persistent aggression from miner birds is one plausible explanation for higher levels of stress among fairy-wrens living in small remnant woodlands.

Chronic stress in fairy-wrens, as indicated by H:L ratio, increased with noisy miner densities within remnant sites. The mean H:L ratio was twice as high at Greenhill than at Tervue, corresponding to an 8-fold increase in densities of noisy miners. Thomson *et al.* (2015) identified a threshold below which the effects of miners on small bird species richness and abundance becomes negligible (0.6 noisy miners ha^{-1}). All of the reserve sites and one woodland remnant site, Tervue, had miner densities lower than this threshold. The H:L ratios of fairy-wrens at Tervue, where miner densities were 0.43 miners ha^{-1}, were only marginally higher than for fairy-wrens living in reserves. Thus, low chronic stress at Tervue is consistent with the impact threshold for noisy miner density proposed by Thomson *et al.* (2015). This study also raises the possibility that even very low numbers of noisy miners could have subtle effects on small birds that have not previously been recognised. The presence of some species of small birds in miner habitat is not sufficient to discount all effects of competition because those birds that persist might still experience chronic stress.

Many studies have demonstrated the negative impact of miners on Australian bird communities at the landscape and habitat patch scale (Piper & Catterall 2003; Montague-Drake *et al.* 2011; Maron *et al.* 2013; Robertson *et al.* 2013). Surprisingly few have studied the effects of competition with miners on the behaviour or physiology of individuals.

In animals with normal physiology, the release of glucocorticoid hormones in response to a stressor is halted by a number of negative feedback loops once that stressor has ceased to operate (glucocorticoids themselves have an inhibitory effect, Romero & Wingfield 2016). Repeated attacks by noisy miners might be sufficient to disrupt normal feedback mechanisms in small birds. Alternatively, birds might associate being attacked with the distinctive vocalisations of noisy miners such that their sound alone could elicit an enduring anticipatory stress response. To test this, future investigations could adopt an experimental approach similar to that of Dantzer *et al.* (2013). To discriminate between the effects of food and competition on stress in red squirrels (*Tamiasciurus hudsonicus*), Dantzer *et al.* (2013) simulated increased population densities of squirrels by broadcasting their sounds. Playing miner vocalisations in remnant woodland could increase the perception of miner densities by small birds and consequently their assessment of risk of being harassed. If H:L ratios among birds exposed to miner playback were higher than for birds exposed to a control noise, this would suggest that miners are indeed a proximate cause of stress in small-bodied birds. In a study of song sparrows (*Melospiza melodia*), simply broadcasting predator sounds led females to lay fewer eggs and provision young less often, ultimately reducing the number of birds reaching independence by up to 53%; stress was not measured directly in that study but it is possible that the response was mediated by stress (Dudeck *et al.* 2018). Miner culls and removal experiments could provide further

opportunities to investigate changes in stress among any resident bird species before and after intervention (O'Loughlin *et al.* 2017; Crates *et al.* 2018).

Body condition as indicated by fat score, and to a lesser degree, the residual mass of fairy-wrens, was negatively correlated with H:L ratio. The metabolic effects of glucocorticoid hormones are generally expected to reduce mass by stimulating gluconeogenesis, lipolysis of fat cells and muscle proteolysis (Sapolsky *et al.* 2000). There was, however, no difference in the residual mass or PCV of fairy-wrens between remnants and reserves, possibly indicating that food availability was not the cause of elevated stress in remnants. Alternatively, birds in remnants may have maintained body weight by foraging more, which could potentially contribute to their higher levels of stress. Amos *et al.* (2013) found no relationship between habitat fragmentation, vegetation condition and haematocrit or residual body mass of several woodland bird species, including superb fairy-wrens. They suggest that such metrics of condition may not be sufficiently sensitive to show any difference caused by habitat change. More responsive methods such as ptilochronology, which involves measuring the growth bars of feathers and indicates a bird's nutritional status, could provide greater insight into variation in condition (Grubb 2006). Factors other than those that we measured, such as age or reproductive status, might have also caused more variation in condition than did stress or perhaps fairy-wrens are well adapted to environmental stressors such that there was minimal impact on their body condition. Superb fairy-wrens are among the most common birds in eastern Australia and can prosper in some urban environments (Parsons *et al.* 2016), suggesting that this species is quite resilient to environmental change.

Animals suffering from chronic stress are thought to have a weakened ability to respond to additional stressors (Romero & Wingfield 2016). Stress can also make individuals more vulnerable to infection by pathogens (Gervasi *et al.* 2016). We found that birds infected by blood parasites (*Haemoproteus* spp.) had higher H:L ratios, but only among fairy-wrens living in reserves. Basal stress levels could already be so high in birds living in remnant habitat that a further stress response cannot elevate levels any higher or perhaps the added stress of infection meant that birds in remnants could no longer persist and simply were not sampled. Curiously, the intensity of infection by *Haemoproteus* was negatively associated with H:L ratio. This pattern appeared to be caused by an increase in lymphocyte numbers and probably reflects a cell-mediated immune response in birds rather than any change in stress. Blue jays (*Cyanocitta cristata*) and great tits (*Parus major*) infected by *Haemoproteus* have been shown to have a higher number of circulating lymphocytes, but only jays had higher numbers of heterophils (Ots & Horak 1998; Garvin *et al.* 2003). We found no relationship between the prevalence of blood parasites and PCV or the mass of birds, a result previously found in other avifauna (Ots & Horak 1998; Kleindorfer *et al.* 2016). Very little is known about the pathogenicity of *Haemoproteus* in Australian birdlife, and populations of wild birds more generally (Adlard *et al.* 2016). This is despite lineages of *Haemoproteus* being found globally and in a diversity of avian hosts (Clark *et al.* 2014). *Haemoproteus* could in fact be relatively benign in superb fairy-wrens.

Birds living in reserves – that is, without miners – were twice as likely to be infected with blood parasites and had higher parasite loads than birds living in woodland remnants on farms. Therefore, without any effect of parasites on stress levels we might have expected more disparate levels of stress between fairy-wrens in remnant and reserve fragments. Reserves probably support a greater range of microhabitats for insect fauna and tended to

have a wetter understorey which was perhaps more suitable for the development of vectors of *Haemoproteus* – bloodsucking dipteran insects (e.g. midges, louse-flies and mosquitos). Studies in Cameroon and tropical Australia also found a higher prevalence of haematozoa among birds living in undisturbed habitats than in deforested areas (Bonneaud *et al.* 2009; Laurance *et al.* 2013). We expected that the prevalence of blood parasites would be low in birds in Tasmania considering the broad trend of decreasing prevalence with distance from the equator (Merino *et al.* 2008), but *Haemoproteus* in our study was more common than previously recorded in birds of both temperate and tropical Australia (Zamora-Vilchis *et al.* 2012; Balasubramaniam *et al.* 2016; Kleindorfer *et al.* 2016). For example, none of 151 fairy-wrens studied in Victoria were infected and *Haemoproteus* was present in just 10.6% of fairy-wrens studied in a South Australian population (Poiani 1992; Colombelli-Négrel & Kleindorfer 2008; Jacques-Hamilton *et al.* 2017). Infection by haemosporidians can be moderated by temperature, altitudinal gradients and landscape features (Sehgal 2015). The relatively high incidence of infection in our study could be related to the proximity of our field sites to waterbodies (farm dams) or to the record levels of rainfall our study region recently received (BOM 2018).

Our results are limited in their interpretation because of small sample size (10-11 birds at some sites where noisy miners were present), which is an inherent consequence of the competitive exclusion of small birds by noisy miners. Several of the remnant woodlands we had initially surveyed supported only one or two fairy-wren territories and almost always of pairs rather than family groups, making it a challenge to identify field sites that would provide statistically viable sample sizes. Fairy-wren territories were generally situated in parts of remnants that provided the most vegetative cover (e.g. near large, spiny shrubs like African boxthorn *Lycium ferocissimum* or gorse) or at the very edge of remnants where

there were fewer tall trees from which miners could harass them. Despite these constraints, our results are consistent with previous studies of birds (Hinam & Clair 2008; Maron *et al.* 2012), mammals (Martínez-Mota *et al.* 2007; Johnstone *et al.* 2012a), and amphibians (Janin *et al.* 2011) that also recorded higher levels of stress (using a range of metrics) among animals living in remnant habitat when compared to more intact environments. Authors of these studies primarily cite reduced food availability associated with habitat fragmentation as a potential explanation for elevated stress. Other explanations given include changes in the movement and locomotion of animals as a consequence of reduced habitat connectivity and more frequent encounters with either conspecifics, predators or humans.

Without information on group size, food availability or predator abundance, which are all factors that might also be correlated with noisy miner density, we cannot definitively attribute the differences in H:L ratio that we observed to the effects of noisy miners. Our results, however, certainly justify further investigation of the effects of competition with miners on physiological stress in small birds. For a full assessment of stress in fairy-wrens occupying noisy miner habitat, stress hormone concentrations could be measured in combination with H:L ratios. This would require the rapid collection of blood samples post-capture but might further develop our interpretation of relationships between H:L ratio and stressors (Johnstone *et al.* 2012b). Metrics of stress are increasingly applied in conservation to predict species persistence, monitor the health of wildlife and as biomarkers of environmental change (Cosgrove *et al.* 2017). Such application demands a sound knowledge of those challenges that elicit a stress response in species. We highlight the potential of interspecific competition, intensified by habitat loss and degradation, to cause chronic stress in Australian avifauna and in wildlife populations more broadly.

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Chapter Five

Low impact of habitat fragmentation and invasive predators on predation of songbird nests in an agricultural landscape.

Scattered paddock trees at "Beaufront".

Abstract

Bird populations are declining in agricultural landscapes globally. An increased rate of nest failure because of changes in abundance of nest predators or vegetation structure could contribute to these declines. We used cameras to monitor nests of two songbirds, the superb fairy-wren (*Malurus cyaneus*) and brown thornbill (*Acanthiza pusilla*), in a highly modified agricultural landscape in Tasmania, Australia. We quantified the three-dimensional structure of vegetation at nest sites using terrestrial LiDAR and tested for habitat effects on daily nest survival rate (DSR) of nests across multiple spatial scales. The local nest-predator assemblage was diverse (14 species) but overall rates of predation were comparable to those in non-agricultural regions. Estimated nest success was 27% based on a combined DSR of 0.956. Birds nested both within the agricultural matrix and in remnant woodlands with mean nest height (30 cm) lower than previously recorded in our study species. Contrary to our expectation, DSR declined with vegetation density at nest sites, was only weakly positively related to extent of woodland cover and was higher for sites with high density of nearby edge habitat These relationships are explained by the habitat preferences of the primary nest predators, which are mostly woodland-dependent native species – the grey currawong, plus other birds, mammals and reptiles – rather than generalists in adjacent farmland such as the feral cat. Birds were more likely to prey on nests that had high levels of surrounding woodland cover, but we detected no other predator-specific relationships with nest-site characteristics. Our results suggest that nest predation may not be an especially significant threat for birds in our study region and that in some Australian songbirds at least, nesting success could be higher in small patches of remnant woodland.

Introduction

Populations of many bird species are declining in agricultural landscapes around the world (Donald *et al.* 2001; Lindenmayer *et al.* 2018; Stanton *et al.* 2018). A long-proposed explanation for these declines is increased frequency of nest failure caused by predation (Wilcove 1985; Angelstam 1986; Valkama & Currie 1999). Conversion of native forests to crops and pasture restricts birds to smaller patches of breeding habitat, potentially causing higher nesting densities and predation rates (Evans 2003). Fragmentation of remaining habitat could promote abundance of nest predators or increase predator activity (Andren 1992; Chalfoun *et al.* 2002; Pita *et al.* 2009), and favour invasive predators such as feral cats (*Felis catus*). At the same time, vegetative cover at nesting sites might be reduced through edge effects including livestock grazing, weed invasion or the removal of coarse woody debris (for example for firewood collection), leaving nests more exposed to predators (Bowman & Harris 1980). Understanding the effects of landscape conversion on the incidence of nest predation requires information both on the effects of habitat features on predation rates, their relative importance, and the predators responsible for nest failure.

Nest success may be influenced by the structure and composition of surrounding vegetation at several spatial scales (Chalfoun *et al.* 2002; Stephens *et al.* 2004; Coates & Delehanty 2010; Robertson *et al.* 2014; Chiavacci *et al.* 2018). At fine scale, plant attributes such as dense foliage or the presence of thorns and spines, may provide concealment or physical protection of nests (Nias 1986; Lambert & Kleindorfer 2006; Colombelli-Négrel & Kleindorfer 2009). Nest height, which can be related to nest predation either positively (Forstmeier & Weiss 2004) or negatively (Hatchwell *et al.* 1999; Beckmann & McDonald 2016), might also depend on the height of available plants. At the microhabitat scale (metres from the nest), surrounding vegetation not only helps to conceal the nest but also

the activities of attending parents. Eggers *et al.* (2008) highlighted this in a study of Siberian jays (*Perisoreus infaustus*). Jay nests built in areas of high vegetation cover had significantly higher parental visitation rates than nests with low cover, suggesting that in some species at least, birds recognise value in nest concealment and trade off levels of parental care against the risk of nest predation. Apart from providing cover, complex vegetation structure at nesting sites can increase search times for predators and so reduce their rate of discovery of nests (Bowman & Harris 1980).

Landscape context and factors at the habitat patch scale can also affect the risk of nest predation (Hartley & Hunter 1998; Zanette & Jenkins 2000; Chiavacci *et al.* 2018). Distance to the edge of a habitat type, typically between closed and open habitats, is the nest-site variable most frequently investigated at this scale (Lahti 2001). Most studies predict lower nest success nearer to habitat edges, because edge habitats might provide sub-optimal nesting opportunities owing to changes in vegetation structure, and because predators may be more abundant or active at the forest edge (Andren 1995; Marini *et al.* 1995; Lahti 2001). Similarly, some studies have found lower nest success in small patches of habitat (Hoover *et al.* 1995; Keyser *et al.* 1998; Burke & Nol 2000), although others have found the opposite (Brooker & Brooker 2001) or no effect of patch size at all (Tewksbury *et al.* 1998; Zanette & Jenkins 2000). Andren (1995) found that edge effects on nest predation were more common in forest patches neighbouring farmland than in other habitat-matrix combinations (for example, native grassland-farmland) but evidence for edge effects on nest predation, in Australian birds especially, remains equivocal (Chalfoun *et al.* 2002; Fulton 2018).

The most relevant scale and relative importance of habitat factors in explaining nest predation depends on the ecology of both the local nest predator assemblage and the focal species of bird (Benson *et al.* 2010; Cox *et al.* 2012; Lyons *et al.* 2015). Varying responses in nest survival to nest height and proximity to edge habitat could be explained by differences in predator type but it is only recently that camera technologies have become widely accessible, allowing researchers to identify predators with accuracy. Nests constructed higher above the ground can be more vulnerable to avian predators while lower nests are most vulnerable to mammalian predators (Hatchwell *et al.* 1999; Piper & Catterall 2004; Remes 2005). Likewise, nest concealment might be effective at deterring only predators that rely on visual cues (i.e. birds) rather than mammalian predators whose primary sense is olfactory (Remes 2005; Colombelli-Négrel & Kleindorfer 2009). Changes in the abundance of nest predators can also result in shifting strategies of nest-site selection because the safest choice of nesting site can be temporally dynamic (Forstmeier & Weiss 2004; Halupka *et al.* 2014).

In this study, we analysed nest predation on two songbirds, the superb fairy-wren (*Malurus cyaneus*) and brown thornbill (*Acanthiza pusilla*) in the Tasmanian Midlands. Our aims were to 1) identify the local nest predator assemblage, 2) model nest survival as a function of habitat variables at multiple spatial scales and 3) test whether habitat predictors of nest success are specific to predator species or class. We chose these study species because previous studies have found high levels of nest predation and diverse nest predators (Rowley 1965; Nias 1986; Mulder 1992; Green & Cockburn 1999; Colombelli-Négrel & Kleindorfer 2009; Guppy 2014; Schneider & Griesser 2014), and we worked in the Tasmanian Midlands because it is a highly modified agricultural landscape with remnant woodlands of varying patch size and vegetation condition We used cameras to record

predation events and identify predators. Some previous studies relied on patterns of nest damage or the use of artificial nests and eggs to infer nest predation and identify predators (Bell & Ford 1986; Gardner 1998; Green & Cockburn 1999; Colombelli-Négrel & Kleindorfer 2009). This can lead to underestimates of nest predation because of differences in scent and temperature that make artificial nests less attractive to predators (Thompson & Burhans 2004), and because of absence of parental behaviours that might either attract or distract nest predators. For example, Kleindorfer *et al.* (2016) showed that female singing behaviour at the nest is associated with a higher incidence of nest predation in superb fairy-wrens.

We used a novel technique – terrestrial Light Detection and Ranging (LiDAR) – to quantify vegetation structure at nesting sites. We predicted that there would be a greater influence of mammalian nest predators in our study region than has been found elsewhere in Australia. This is because the feral cat is highly abundant in this region (Hamer 2019), and is a significant predator of birds elsewhere in Australia (Woinarski *et al.* 2017), while native mammalian predators are also common; these native predators include species that are rare (e.g. spotted-tailed quoll *Dasyurus maculatus*) or extinct (Tasmanian devil *Sarcophilus harrisii*) on the Australian mainland. We further predicted that survival would be higher for nests that were well-concealed and surrounded by complex vegetation, because such nests would be less exposed to predators.

Methods

Study area and species

The Tasmanian Midlands (Fig. 5.1) is an agricultural landscape retaining only 10% of its original temperate woodlands and 3% of native grasslands (Fensham 1989; Jones & Davidson 2016). Sheep grazing is the primary land use, but pastures are increasingly being

converted to intensive cropping of cereals, vegetables and oilseeds (Prior *et al.* 2013). The region is recognised as one of 15 National Biodiversity Hotspots, owing to a high level of species endemism and the presence of threatened flora and fauna (Cowell *et al.* 2013).

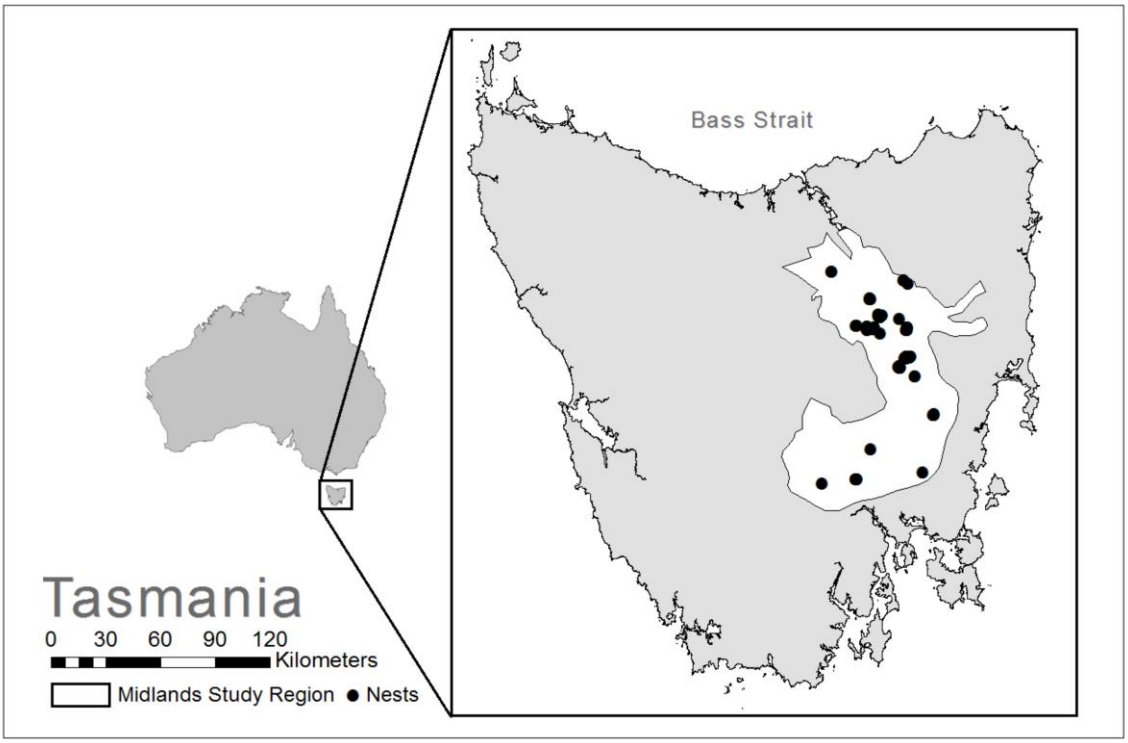

Figure 5.1. The locations of superb fairy-wren and brown thornbill nests found within our study region, the Midlands of Tasmania (inset), Australia.

Superb fairy-wrens and brown thornbills are small insectivorous passerines that are common in south eastern Australia, including Tasmania. They are sedentary, defend territories year-round and build domed nests that are typically well hidden in low, dense vegetation (Rowley 1965; Green & Cockburn 1999). Thornbill territories range from 0.3 to 3.5 ha and fairy-wren territories from 0.6 to 8.6 ha (Bell & Ford 1986; Mulder 1992; Chan & Augusteyn 2003). Thornbills breed in pairs and are sexually monomorphic. Superb fairy-wrens are sexually dichromatic and cooperative breeders in which all members of a family group contribute to provisioning of young (Dunn *et al.* 1995). Many of the territories in our

study, however, appeared to support only pairs rather than groups. Females of both species build nests and incubate eggs without assistance, lay clutches of 2-4 eggs, and can have several nesting attempts within a season (Rowley 1965; Green & Cockburn 1999). The incubation and nestling periods are about 14 and 12 days respectively for fairy-wrens (Rowley 1965; Colombelli-Négrel & Kleindorfer 2009), 18 and 16 days for thornbills (Green & Cockburn 1999).

Data collection

We searched for nests opportunistically between August and February over two breeding seasons (2015 & 2016). We did not restrict nest searches to particular habitat types but rather attempted to locate and monitor as many nests as possible across the geographical range of our study region. Nests were located by observing the behaviour of nest-building or incubating females and adults on regular feeding runs to nestlings. On three occasions, nests were located by inadvertently flushing an incubating female. When a nest was first located, we recorded its height above ground and position using a GPS. We also noted the stage of the nest as either: 1) building, 2) nest lined but empty, 3) eggs present or 4) nestlings present.If eggs or nestlings were already present, we counted their number and identified any cuckoo eggs or young via visual inspection (size and colouration of eggs, zygodactyly of nestlings).

To identify nest predators and their behaviour, we positioned infrared motion-sensor cameras (PC800 Reconyx HyperFire) 1-3 m from each nest. These were secured at nest height to an adjacent tree when available or otherwise to a wooden picket. For nests located on the ground, cameras were concealed beneath woody debris. If the nest was still being built we waited until the first egg was laid before placing a camera to minimise the

risk of nest abandonment. Cameras were set to 'rapid-fire', taking 10 photos each time they were triggered. Nests, and therefore cameras, were widely dispersed both spatially and temporally, reducing the potential for predators to learn of their association. Previous studies have found no effect of camera presence on the incidence of nest predation (Coates & Delehanty 2010; Guppy 2014) or else a positive effect of cameras on survival (Richardson *et al.* 2009). We never altered vegetation cover at nesting sites, meaning an uninterrupted view of the nest contents was not always possible. Nests were approached only in the absence of potential nest predators (e.g. currawongs and kookaburras) and for short periods (< 1 minute).

We revisited nests every 3-7 days to record their contents and check that cameras remained focussed and had sufficient space on memory cards. Nest checks varied in frequency because of limited access to private property and flooding events. Predation was characterised by the disappearance of eggs or nestlings from nests before the expected fledging date or by direct signs including eggshells, dead nestlings or nests that were misshapen and destroyed. Nest predation and brood parasitism were usually confirmed by the presence of predators and cuckoos on camera images. Nest fate was recorded as successful if one or more young fledged, excluding cuckoo chicks. Apart from predation events, we also used camera images to record predators that passed by nests or that interacted with the nest without preying on nest contents (Maziarz *et al.* 2018). "Passes" were scored if a potential nest predator came within one metre of the nest. We did not include the eastern bettong (*Bettongia gaimardi*) as a potential nest predator, though other *Bettongia* species have been found to prey on artificial nests (Fulton 2017). For every predation event or predator pass, we noted the time and date on the camera image.

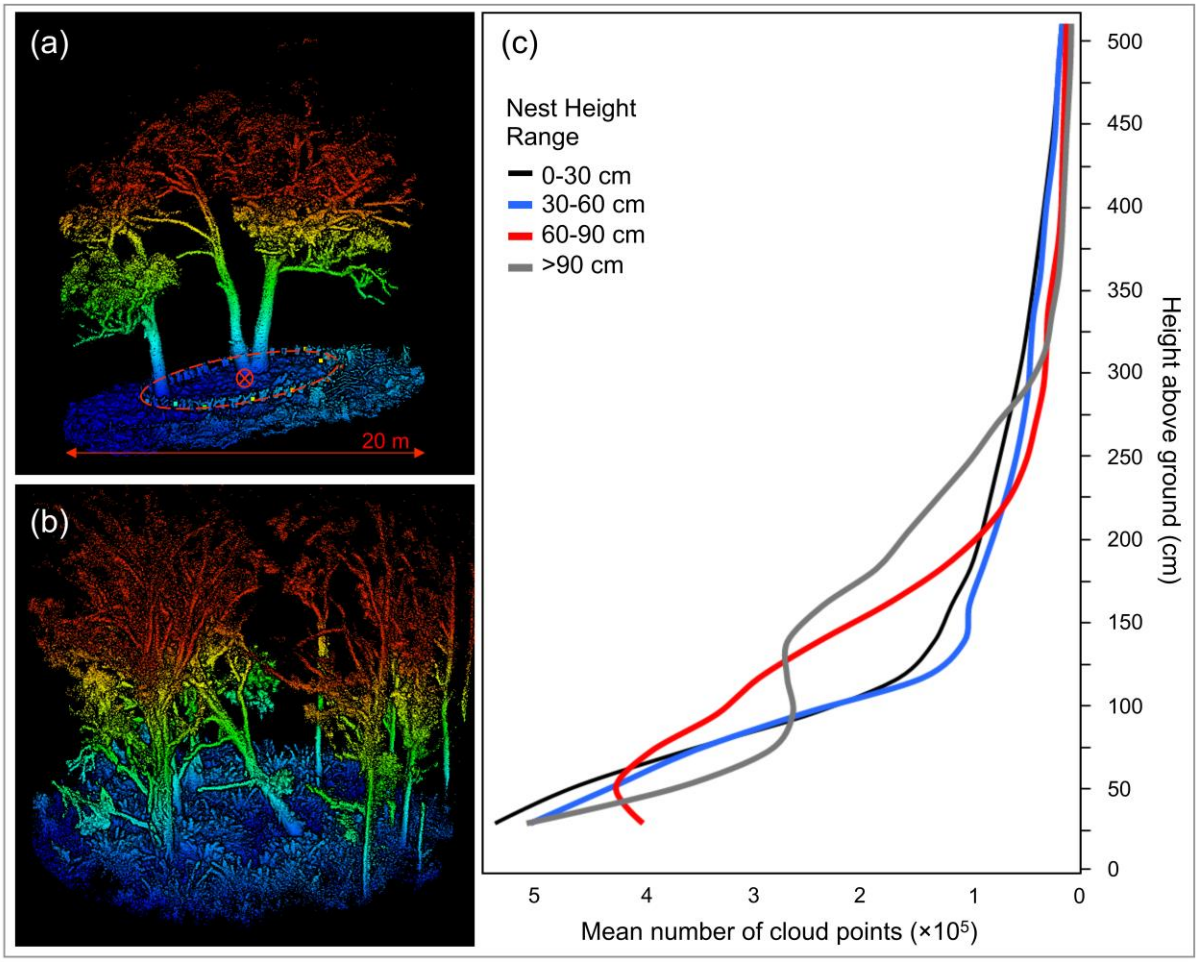

Figure 5.2. (a) and (b) are examples of point clouds collected using terrestrial LiDAR and depict the three-dimensional vegetation structure at nesting sites. The colour of cloud points indicates their height above ground. The path walked to collect LiDAR data, a circle of 5 m radius centred on the nest, is shown in (a). Point clouds were clipped to 20 m diameter before extracting the habitat variables described in Table 5.1. (c) shows the vertical profile of vegetation structure at nesting sites (up to 5 m above the ground) as represented by the number of cloud points. Each line specifies the average profile of nests built within four height ranges.

When a nest was vacated (fledged, abandoned or depredated) we used terrestrial LiDAR (ZEB1) to produce a point cloud that depicted the three-dimensional physical structure of the surrounding vegetation and woody debris. A point cloud is a collection of LiDAR returns (Fig. 5.2). These returns were generated while carrying the LiDAR system and

walking slowly in a circle of five metre radius around the nest (Fig. 5.2a). After normalising the LiDAR data against ground points, which were later removed, we clipped the point cloud to a 10 m radius from the nest. Thus, all habitat variables derived from LiDAR data were calculated from a cylinder centred on the nest with dimensions equal to 20 m diameter and length equal to the tallest vegetation at the nest site. We used lascanopy of LAStools (Isenburg 2017) to compute several height metrics that reflected vegetation density or "clutter" at nest sites and were considered to model habitat structure from the perspective of both birds and their nest predators.

We also recorded the species and height of the nest plant, canopy closure above the nest, nest concealment and nest state. Canopy closure was calculated using fish-eye photography and the software program Gap Light Analyzer (Frazer *et al.* 1999). Nest concealment was estimated as the mean proportion of the nest visible from above and to the sides of the nest from a distance of one metre. We used photographs of a white polystyrene sphere (10 cm diameter, approximately the same size as nests) that was positioned in place of the nest and repurposed Gap Light Analyzer to calculate accurate measures of vegetation covering the sphere (or nest) at this scale. We also photographed nests *in situ* in the same manner. Nest state described whether the nest was intact, the lining was removed, holes were present in the nest walls, entrances were enlarged, nests were tipped or repositioned, and the presence of unhatched eggs or eggshells. Finally, we used satellite imagery and ArcMap (version 10.4.1, ESRI 2019) to measure habitat characteristics at the landscape scale. This included woodland cover and the density of edge habitat within three spatial scales surrounding the nest. Full descriptions of all habitat variables are provided in Table 5.1.

Table 5.1. Nest-site and landscape level habitat variables measured at superb fairy-wren and brown thornbill nests in the Tasmanian Midlands. Provided are the mean values ± standard error and the range of values measured for each variable.

Variable	Description	$\bar{x}$ ± se	Range
Nest-site			
Height	Height of the nest above ground (cm). Measured to the base of the nest.	29.56 ± 3.43	0 - 159
Canopy Height	Height (m) of the tallest vegetation within a 10 m radius of the nest. Determined from LiDAR data.	14.43 ± 0.57	1.67 - 22.74
Canopy Closure	Canopy closure (%) immediately above the nest.	34.59 ± 2.36	0 - 80.94
Concealment	Average proportion of the nest visible (%) from above and to the sides of the nest.	18.15 ± 1.56	0 - 67.74
Skew	Skew of LiDAR cloud points within a 10 m radius of the nest. Reflects the vertical distribution of vegetation 'clutter' surrounding the nest.	2.30 ± 0.19	0.28 - 12.48
Points > 1.5 m	Total number of LiDAR cloud points below 1.5 m ($\times 10^5$) within a 10 m radius of the nest. Reflects structural complexity of vegetation at nesting sites within the range of the highest nest that we found.	15.46 ± 0.74	3.99 - 35.12
Points Nest	Number of LiDAR cloud points ($\times 10^5$) within the 30 cm vertical interval at which the nest was built.	4.87 ± 0.22	0.03 - 10.33
Landscape			
Distance to Edge	Distance (m) to the nearest habitat edge. When nests were built within the agricultural matrix, distance to edge was recorded as zero metres.	135.55 ± 16.56	0 - 550.98
Woodland Cover	Total cover (%) of native woody vegetation and eucalypt plantings (productive and mixed species). We measured woodland cover within 500 m, 100 m and 50 m buffer zones around the nest.	*500 m* 56.88 ± 3.84 *100 m* 73.64 ± 3.66 *50 m* 80.50 ± 3.57	0.20 - 100 0 - 100 0 - 100
Edge Density	Sum of the total length (m) of edge habitat within 500 m, 100 m and 50 m buffer zones around the nest.	*500 m* 2347.68 ± 155.6 *100 m* 112.50 ± 14.67 *50 m* 34.08 ± 7.20	0 - 5970.49 0 - 427.87 0 - 393.96

Nest survival analysis

We used the nest survival model in the software program MARK 9.0 (White & Burnham 2009) and the package RMark (Laake & Rexstad 2008) in program R version 3.4.0 (R Development Core Team 2017) to test the effects of habitat variables on daily survival rates (DSR) of nests. We did not include re-nests in our analysis. Dates were scaled such that 1 denoted the day that our first nest was found to be active (eggs present) and a 156-day nesting season was consequently defined. MARK employs maximum likelihood to produce

estimates of DSR and ranks competing models of DSR using an information theoretic approach. We used Akaike's information criterion corrected for small sample size (AIC*c*) to select the most parsimonious models.

Model development was performed in four stages. First, we assessed correlations among habitat variables to avoid including correlated variables ($|r| > 0.6$) in the same model. Second, we ran univariate models of DSR that included the effects of year (2015/16 or 2016/17) and day of the breeding season but found no support for either variable; the null model (constant DSR) produced the lowest AIC*c*. We then excluded temporal variables from subsequent analyses and pooled nests from both breeding seasons. Third, we investigated the relationship between DSR and habitat variables at the nest-site level. We produced a list of 15 *a priori* candidate models (Appendix C.1) that included single terms as well as combinations of covariates (additive and interactions). We retained only those variables included among models that performed better than the null (i.e. lower AIC*c*). Only two nest-site variables, nest height and cloud points < 1.5 m, and their additive effect were retained in the final stage of model development.

We combined the selected nest-site variables with landscape-level habitat characteristics to produce a final candidate set of 20 models (Table 5.2). Among this set were models that varied only in the spatial scale at which woodland cover and edge density were measured. This was intended to identify the best scale for the relationship between these variables and nest survival. Distance to edge was correlated with woodland cover at the 100 m and 500 m spatial scales and so these variables were never included in the same model. Based on field observations and previous literature, we predicted that the influence of nest height on DSR might vary with distance to edge, or the density of edge habitat and

so included the relevant interaction terms among models in our final suite. We present results from this final stage of our survival analysis, and parameter estimates with 95% confidence intervals that are derived from the top performing model.

Predator type analysis

We classified nest predators and brood parasites into birds, snakes and mammals. Each predator class was expected to utilise a different search strategy, birds being visually oriented, snakes using thermal cues and mammals being mainly olfactory predators. Cuckoos were treated the same as avian nest predators because we observed them both removing eggs from nests and parasitising nests. To examine the relationship between habitat variables and predation by predators of a given class, we fit a one-way ANOVA to each normally distributed variable. For habitat variables with a highly skewed distribution or with outlier observations, we used Wilcoxon rank sum tests.

Results

We monitored a total of 84 nests: 41 brown thornbill and 43 superb fairy-wren nests. The outcome of five nests was unclear due to interference with cameras by brushtail possums (*Trichosurus vulpecula*), extreme weather events and camera failure during the late stages of the nestling period. Of the remaining 79 nests, 36 (46%) failed because they were depredated (42%) or parasitised by cuckoos (4%), 12 (15%) were abandoned and 31 were successful (apparent nest success = 39%). One fairy-wren nest was parasitised by a cuckoo but was nonetheless successful because the female fairy-wren buried the cuckoo egg beneath nesting material and laid her eggs on top, from which three nestlings later hatched and fledged. Sixteen nests had clutches of four eggs (mean clutch size = 3.38 ± 0.07) in the

2016/17 breeding season but there were no four-egg clutches in 2015/16 (2.95 ± 0.05). We excluded all abandoned nests and nests with unknown outcome from subsequent analyses.

The estimated DSR for both fairy-wrens and thornbills combined was 0.956 (95% CI, 0.94-0.97). Based on a weighted average of each species' nesting period, the point estimate of survival was 27%. DSR for thornbills alone was 0.954 (95% CI, 0.93-0.97), giving a point estimate of nest survival of 21%. DSR for fairy-wrens was very similar, 0.959 (95% CI, 0.94-0.97), but because of their shorter nesting period (~26 days *versus* ~34 days) the associated estimate of survival was 33%.

Table 5.2. Summary of results from the final stage of model selection predicting daily nest survival rates in superb fairy-wrens and brown thornbills in the Tasmanian Midlands. Models are ranked by AIC*c* and include nest-site variables at the landscape and microhabitat scales. A full description of habitat variables is available in Table 5.1.

Model	*K*	AIC*c*	Δ AIC*c*	ω_i	-2Log(*L*)
Height × Edge 100 + Wood 100 + Points 1.5	6	271.25	0.00	0.48	259.14
Height × Edge 100 + Wood 500 + Points 1.5	6	272.82	1.57	0.22	260.72
Height + Edge 100 + Wood 100 + Points 1.5	5	275.25	4.00	0.07	265.18
Height × Edge 100	4	275.36	4.11	0.07	267.31
Height × Distance Edge + Edge 100 + Points 1.5	6	275.61	4.36	0.05	263.50
Height × Edge 100 + Wood 100	5	277.04	5.79	0.03	266.97
Height × Distance Edge	4	278.25	7.00	0.01	270.20
Height × Edge 50 + Wood 100 + Points 1.5	6	278.57	7.32	0.01	266.47
Height + Points 1.5	3	279.10	7.85	0.01	273.07
Height + Edge 50 + Wood 100 + Points 1.5	5	279.14	7.89	0.00	269.06
Height + Edge 100 + Wood 500 + Points 1.5	5	279.58	8.33	0.00	269.51
Points 1.5	2	280.08	8.83	0.00	276.07
Height	2	280.30	9.05	0.00	276.28
Height + Wood 100 + Edge 100	4	280.36	9.11	0.00	272.30
Height + Edge 100	3	280.53	9.28	0.00	274.50
Null	1	280.72	9.47	0.00	278.72
Height + Wood 500 + Points 1.5	4	280.83	9.58	0.00	272.78
Wood 100 + Edge 100	3	281.00	9.75	0.00	274.97
Wood 500 + Edge 100	3	281.72	10.47	0.00	275.69
Height × Edge 500 + Wood 500 + Points 1.5	6	284.01	12.76	0.00	271.91

The most parsimonious model of DSR (Table 5.2) included a negative effect of the number of cloud points (vegetation density) below 1.5 m (-0.080, 95% CI [-0.135, -0.024], Fig. 5.3), a modest positive effect of woodland cover within 100 m (0.009, 95% CI [-0.005, 0.022]) and an interaction between edge density at the 100 m scale and nest height : DSR increased with the density of edge habitat but only for nests built close to the ground while the positive effect of nest height on DSR was much stronger at sites with low edge habitat (Fig. 5.4). The second-best model, which was within 2 Δ AIC*c* units, was identical except that woodland cover at the 500 m scale was included rather than at 100 m. All other models had an AIC weight of 0.07 or less.

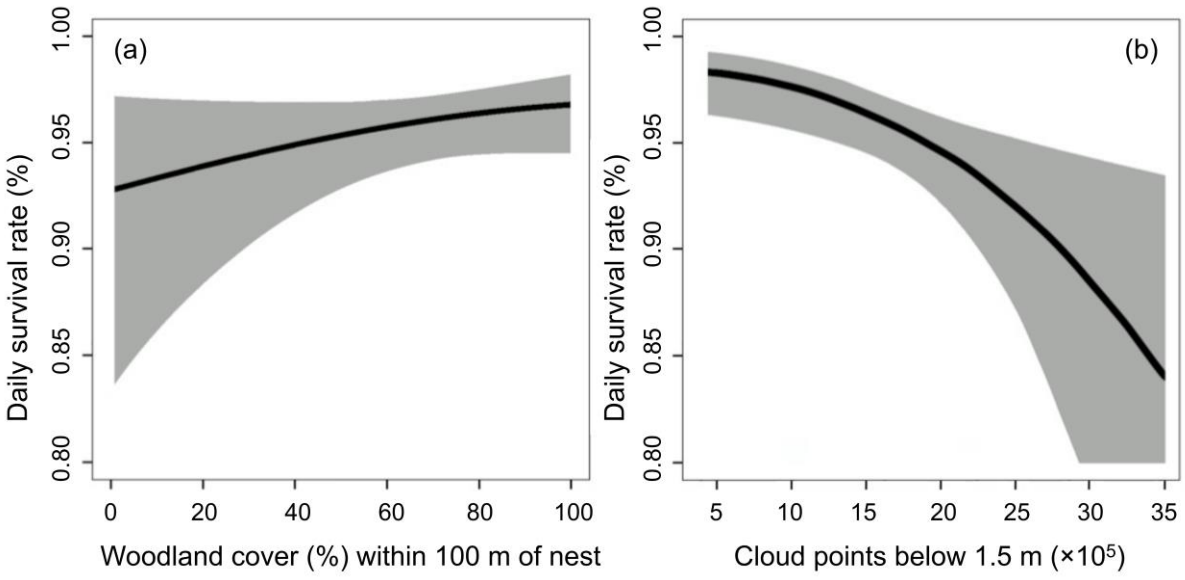

Figure 5.3. Model predicted daily survival rate of brown thornbill and superb fairy-wren nests in relation to (a) the amount of woodland cover within a 100 m radius and (b) the number of LiDAR cloud points below 1.5 m and within a 10 m radius – a proxy for vegetation density. Shaded areas indicate 95% confidence intervals.

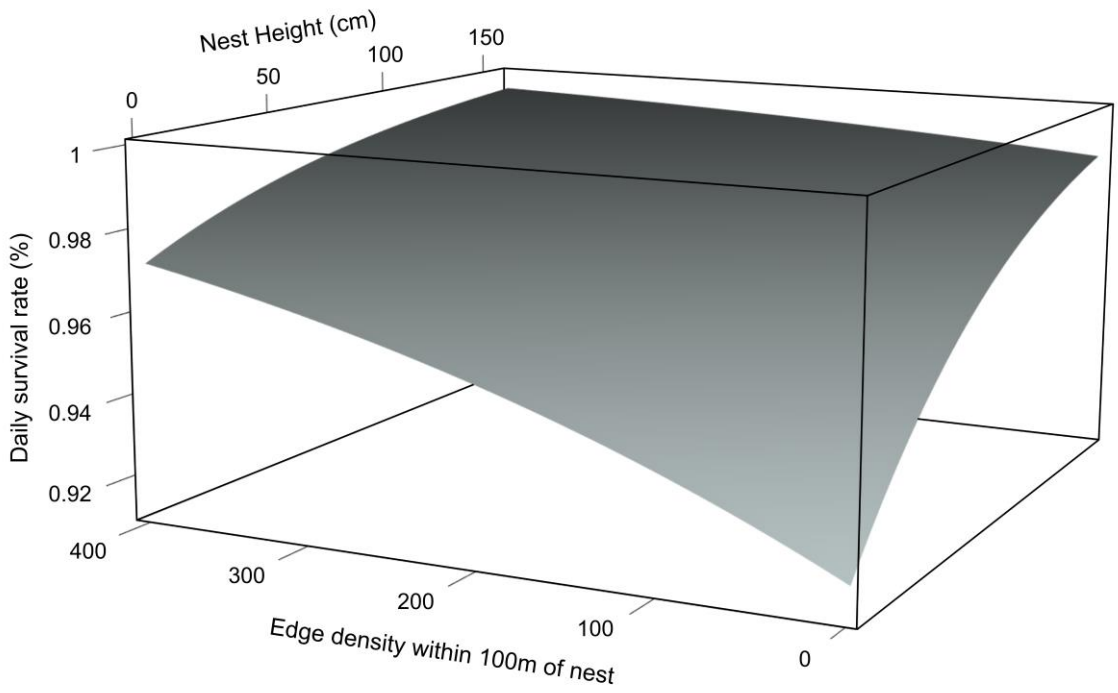

Figure 5.4. An interaction effect between the density of edge habitat within a 100 m radius of nests and their height on daily survival rate (%) of superb fairy-wrens and brown thornbill nests in the Tasmanian Midlands.

Nest site selection

Mean nest height was 29.56 cm but ranged from 0 cm (on the ground) to 159 cm. One-third of all nests were built below 10 cm. LiDAR data showed that most of the vegetation at nesting sites was low to the ground and vegetation density quickly dropped off above ~60 cm in height (Fig. 5.2c). Only three nests were built above one metre; all were in the invasive weed gorse (*Ulex europaeus*) and all successfully fledged young. The profile of point clouds at these nests showed that vegetation density was much higher 1-2 m above the ground when compared to other nesting sites (Fig. 5.2c). The highest-built nest was constructed on top of an open-cup European goldfinch (*Carduelis carduelis*) nest.

Most nests were built in swards of spiny-head mat-rush (*Lomandra longifolia*, *n* = 27) followed by other species of native and introduced grasses (e.g. *Poa labillardieri*, *P. rodwayi*, *Elymus scaber*, *Phalaris aquatica*, *Lolium perenne*, *n* = 15), native bracken fern (P*teridium esculentum*, *n* = 9), native shrubs (e.g. *Hymenanthera dentata*, *Melaleuca gibbosa*, *Acacia verticillata*, *Cassinia aculeata*, *Ozothamnus aculeata*, *n* = 8), gorse (*n* = 7), sedges (*Lepidosperma* spp., *n* = 7), heathy native groundcovers (e.g. *Lissanthe strigosa*, *n* = 4), among woody debris (*n* = 4), and in introduced thistles (*Silybum marianum* & *Cirsium vulgare*, *n* = 3).

Nest predators

We identified 14 different nest predators and brood parasites. The most common predator was the grey currawong (*Strepera versicolor arguta*, *n* = 6), followed by feral cat, spotted-tailed quoll and tiger snake (*Notechis scutatus*, *n* = 3 nests each), lowland copperhead snake (*Austrelaps superbus*), brushtail possum and fan-tailed cuckoo (*Cacomantis flabelliformis*, *n* = 2 nests each). A single nest each failed because of predation by black rat (*Rattus rattus*), brown goshawk (*Accipiter fasciatus*) and Tasmanian devil or brood parasitism by a cuckoo, one each of shining-bronze cuckoo (*Chrysococcyx lucidus*) and Horsefield's bronze cuckoo (*Chalcites basalis*). One nest was partially depredated by two species, a grey butcherbird (*Cracticus torquatus*) and house mouse (*Mus musculus*).

Predators of 8 nests could not be identified because they were either obscured by vegetation or because cameras failed to trigger. One of these nests had a neat, circular hole in the back of the nest wall, a pattern that has been attributed both to predation by snakes and mice (Brooker & Brooker 2001; Colombelli-Négrel & Kleindorfer 2009). Another nest was destroyed at night, probably by a cat or quoll, but tall grass made identification

impossible. Finally, one camera had moved such that it was no longer focussed on the nest. A spotted-tailed quoll, grey currawong and feral cat were all recorded within a short period of time within two metres of the nest, but we were unable to determine which predator was responsible for nest failure.

Camera images and data from nest checks indicated that, on several occasions, grey currawongs only partially removed nest contents. Thus, it is uncertain whether some nests were raided by several currawongs or the same individual on different occasions. This was particularly the case for one thornbill nest which was inspected by a currawong on at least five occasions, but where only one nestling was removed at a time (three in total) over a period of two weeks; the last surviving nestling was very close to its expected fledging date. A fan-tailed cuckoo was recorded removing fairy-wren eggs from a nest before daybreak. In one instance, a feral cat that had been fitted with a GPS collar by another researcher in a concurrent study (Hamer 2019), became aware of a superb fairy-wren nest only after inadvertently bumping into the plant in which the nest was located. This movement caused the ~9-day old nestlings to leave their nest, at which point the cat caught and ate them from the ground.

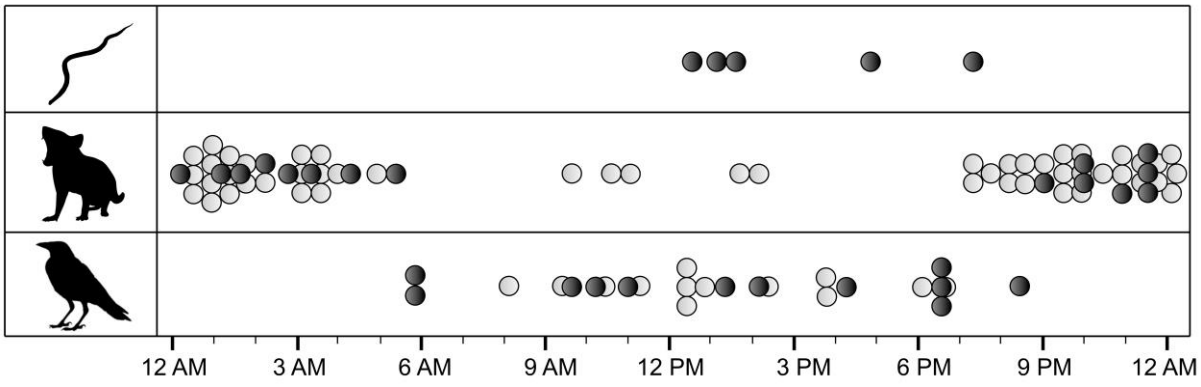

Figure 5.5. Time of nest predation events (black circles) and predator passes (grey circles) by snakes, mammals and birds at nests of superb fairy-wrens and brown thornbills.

Mammals more frequently passed nests than did birds and snakes (Fig. 5.5). Snakes were observed in camera images only when they were raiding a nest. An Australian magpie (*Cracticus tibicen*) and grey-shrike thrush (*Colluricincla harmonica*) were recorded inspecting nests just hours after they had been depredated by another animal. Nests were visited by mammalian predators throughout the night and by birds and snakes during the day (Fig. 5.5). Birds were more likely to depredate nests in areas of high woodland cover (Fisher's exact test, $p = 0.003$) than nests in areas with low woodland cover (< 50% at the 500 m scale). Wilcoxon rank sums tests also showed that birds were more likely to depredate nests than mammals ($z = -2.00$, $p = 0.045$) and snakes ($z = -2.27$, $p = 0.023$) and that this effect was associated with increasing levels of wooded cover. We found no evidence for any other relationships between habitat variables and predator class.

Discussion

We monitored nests of superb fairy-wrens and brown thornbills in a heavily modified agricultural landscape with very high densities of feral cats (Hamer 2019) and other mesopredators. Nonetheless, we found that overall nest success of both species was comparable to previous studies in less disturbed landscapes (apparent nest success = 19% Bell & Ford 1986; 38% Green & Cockburn 1999; 21% Colombelli-Négrel & Kleindorfer 2009; 33% Schneider & Griesser 2014). Our estimate of apparent nest success was identical to that of Nias (1986, 39% of 116 clutches) who studied superb fairy-wrens in a large patch of disturbed woodland, and Mulder (1992, 39% of 343 clutches) who studied them in high-quality habitat. Most predation of nests was by native predators, mostly by birds, and predation rates were higher in larger, more intact patches of woodland than in small remnant woodlands and highly disturbed sites. Most studies predict negative effects of edge

habitat on nest survival (Paton 1994; Lahti 2001) but the preference of predators for woodland cover contributed to the opposite effect in this study.

While overall nest success was similar to that previously recorded in wrens and thornbills, nest-site selection, habitat features influencing daily survival rate of nests, and the predators responsible for nest failure appear to differ on farms in the Midlands. For example, data from the Australian Nest Record Scheme (Higgins & Peter 2002) indicate an average nest height of 78 cm for brown thornbills (range 0 - 800 cm, *n* = 497) and 66 cm for superb fairy-wrens (0 - 560 cm, *n* = 1169) but mean nest height was just 30 cm in this study with one-third of all nests built below 10 cm. This reflects the loss of midstorey vegetation, particularly native shrubs, throughout much of our study region. When available, tall and prickly invasive plant species were used for building nests and may have offered extra protection against predators.

Agricultural intensification typically results in the broad simplification of landscapes and is expected to favour generalist predators, particularly invasive species. Feral cats and large open-country birds such as ravens (*Corvus tasmanicus*), kookaburras (*Dacelo novaeguineae*), butcherbirds and magpies (*Cracticus* spp.) have benefitted from better access to food (livestock carrion and soil invertebrates) and changes in vegetation structure in the Midlands (Chapter Three, Hamer 2019). Cats are known to preferentially forage at woodland edges and in linear vegetation such as shelter belts – habitats typical of agricultural landscapes (Doherty *et al.* 2014; Hamer 2019). Farm infrastructure (farm sheds and weedy fence lines) might also harbour rodents who are capable of preying on nests (Singleton *et al.* 2007). However, we found that most nest predation was by native predators that prefer large patches of woodland. The most common predator was the grey

currawong, a native species associated with large patches of relatively intact woodland in our study region (Chapter Three). In contrast, ravens were never observed raiding a nest despite their numbers having significantly increased over the last two decades (Cunningham *et al.* 2018). Many of the other nest predators we recorded are also woodland-dependent (e.g. spotted-tailed quoll, fan-tailed cuckoo). There is no evidence that grey currawongs, or the other bird species identified as nest predators, have recently increased in abundance in the Midlands (Chapter Three). Feral cats were pervasive throughout the landscape with one cat eating eggs from a nest built in the centre of a large (> 360 ha) woodland.

Nests built in areas with low densities of edge habitat had high predation rates, but the reasons for this varied. Some nest sites were low-edge because they were near the centre of large to medium-sized woodland patches. Such nests were probably exposed to a higher abundance of predators, particularly native woodland species, and therefore had lower daily survival rates. This is consistent with the results of Brooker and Brooker (2001) who found that nest survival of blue-breasted fairy-wrens (*Malurus pulcherrimus*) in the wheatbelt region of Western Australia declined with increasing patch size. They did not identify nest predators in that study but suspected that larger patches of woodland harboured more predators.

Other were associated with low density of edge habitat because they were built in isolated shrubs and weeds in the agricultural matrix. Being highly exposed, these were quickly located by terrestrial predators (as revealed by camera data), including snakes, possums, cats and a rat, but were less likely to be found by avian predators. One nest was also very nearly destroyed by a tractor mounted slasher. The relatively larger influence of terrestrial predators on nests built close to the ground could explain the interacting effects

of nest height and edge density on nest survival, as nests with low edge densities, either in paddocks or in large woodland patches, were more successful when built higher in vegetation.

Concealment of nests by vegetation was evidently unrelated to their fate. This is surprising considering the effort that both fairy-wrens and thornbills invest in cryptic nest placement among low, dense vegetation. Colombelli-Négrel and Kleindorfer (2009) found a positive effect of concealment on nest success in fairy-wrens (although characterising concealment using a different method to ours). Concealment may be a useful predictor of nest survival only when comparing nests in the same habitat type or habitat patch; otherwise differences in edge density or vegetation structure might mask any influence of nest concealment. Colombelli-Négrel and Kleindorfer (2009) attributed 50% of nest predation in their study to rodents but this was based on patterns of nest destruction. Our study and others (Thompson & Burhans 2003) showed “nest state” to be a fraught technique for identifying predators, because methods of removing nest contents vary among conspecifics. One feral cat left the nest entirely intact with only egg shells remaining, another enlarged the nest entrance; spotted-tailed quolls either left nests intact or removed their entire top half. We also recorded both fairy-wrens and thornbills re-using nesting materials after their nests were depredated. Two females did this methodically, leaving half of the nest intact and removing only the front (which then resembled an open-cup nest turned on its side) while another destroyed her nest completely, leaving a mess of nesting material scattered over the forest floor. Because of these factors, it is plausible that nest predation was mis-attributed in earlier studies. The lack of an effect of nest concealment in our study could reflect a higher proportion of depredation by nocturnal mammals (15/32

predation events recorded, 47%) that use olfactory sense to locate nests or perhaps grey currawongs rely more on aural cues from nestlings and parents rather than sight.

Contrary to our prediction that nest success would inrease with density of surrounding vegetation, we found that DSR declined with increasing density of LiDAR cloud points within a 10-metre radius of the nest. Possibly, dense vegetation at nesting sites reflects the quality of the surrounding woodland and is therefore positively related to predator density, offsetting the benefit from slowing predator searches. Structural habitat elements near to nests can also directly harbour nest predators or support their activities. For example, With (1994) found that nests of the McCown's Longspur (*Calcarius mccownii*) next to shrubs were 2-3 times more likely to be depredated by ground squirrels. It is also possible that dense vegetation lessens the ability of birds to detect and respond to an approaching predator (Lima 2009), although this effect may be small in our study because super fairy-wrens and brown thornbills are largely unable to defend their nests against predators; superb fairy-wrens can perform a 'rodent-run' to gain the attention of predators (Rowley 1962) but it is unlikely that this alone could explain such a strong negative relationship between DSR and vegetation density.

There is a need to better understand the importance of different nest predators in Australian woodlands (Fulton 2018). This is especially because assemblages of nest predators vary with location, even when concerning the same habitat type (Guppy *et al.* 2017). We expected that feral cats would pose a serious threat to nesting birds in the Midlands, because of evidence that cats are significant predators of birds throughout Australia (Woinarski *et al.* 2017), and because densities of cats are very high in the Midlands (Hamer 2019). However, we found that cats were not a predominant predator of nests,

accounting for only 11% of all predation events. They were no more significant than native species such as the spotted-tailed quoll and tiger snake and were less important than native birds. While it remains possible that cats are major predators of juvenile and adult birds in this landscape, our results suggest that feral cats are not important in limiting breeding success of songbirds. Control of feral cats is therefore unlikely to lead to significantly increased nest success in this system.

Our results suggest few avenues for management of habitat structure to promote nesting success in the Midlands. Restoring structural complexity of midstorey vegetation could provide birds with higher nesting opportunities and improve nest survival at some sites but this might equally benefit the local nest-predator community, which is highly diverse. Because of this diversity, predators are likely to respond to habitat structure around nests in a variety of ways and at various scales, making it unlikely then that any single strategy of nest-site selection by birds, or manipulation of nesting habitat by managers, would lead to increased nest success. Further, our cameras revealed that nests were preyed on throughout the night and day, meaning that the capacity for behavioural adaptations to compensate for nest predation risk (e.g. adjustment of feeding rate to nestlings) might also be limited (Lima 2009).

A number of nests were inspected by predators after they had already been depredated or young had fledged, highlighting that activity at the nest is not necessary for predators to locate nests. Most studies of nest predation have failed to consider that nests could be visited by multiple predators and of different species, but our results suggest the assumption that nests are depredated entirely by a single predator may not always be accurate. An interesting area for future study is the possibility that individuals of predators

like currawongs may return to raid nests on multiple occasions, analogous to caching of food.

Conclusions

Nest predation rates are increasing among Australian songbirds (Remeš *et al.* 2012). Our results do not support the view that this increase is caused by habitat fragmentation in landscapes converted to farming, or by intensified predation by feral cats or other invasive predators. In the Midlands region at least, we should look to other life-stages or habitat effects to account for bird decline. Other processes such as food scarcity in converted habitats (Watson 2011) could be causing bird declines in the Midlands and management actions might be better focussed on these. Having said this, the loss of vegetation structure typically associated with farm management practices could still have indirect effects on the reproductive success of birds (for example through changes in food abundance, Dunn et al. 2010). Further research is needed to clarify how the nest predator community of the Tasmanian Midlands might differ from those in non-agricultural landscapes and indeed for other local bird species (e.g. open-cup nesters). We suggest that mammalian predators and snakes could play a proportionately higher role in landscapes with low native vegetation cover but, apart from cats, there is no evidence to suggest that any of the nest predators that we identified are increasing in number or activity in our study region. Invasive weeds like gorse and thistles offered good nesting habitat for our study species, both in and out of woodland patches. Land managers should more often consider the value of weeds for nesting birds in landscapes that are largely cleared of native vegetation. Finally, the common view is that large areas of woodland are crucial for conservation in agricultural landscapes (Wintle *et al.* 2019). There are many reasons why this might be true, but our results suggest that at least in some Australian songbirds nesting success might be higher in

smaller patches of woodland, especially those with diverse vegetation that provides food resources and nesting opportunities.

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Chapter Six

General Discussion

A winter's day at "Saint Peters Pass".

Thesis Summary

In the thesis, I assessed patterns of community composition, species abundance and occupancy of birds in the Tasmanian Midlands and how this has changed in response to differences in land use over the past 20 years. I also tested two potential mechanisms of avifauna loss from this highly-modified agricultural landscape: physiological stress caused by aggressive competition with a native honeyeater; and increased rates of nest predation due to habitat fragmentation and degradation or a greater influence of mesopredators.

The results of my study of bird communities (Chapter Three) are consistent with relationships between bird species and environmental factors that have previously been identified elsewhere in Australia and in the earlier study of woodland birds in the Midlands (MacDonald 2001). Woody vegetation cover, elements of structural complexity (e.g. foliage projective cover and leaf litter) and the abundance of noisy miners all influence community composition. As expected, agricultural intensification in the Midlands has resulted in greater numbers of large bird species that feed on crops (e.g. cockatoos and galahs) and generalists that forage in paddocks (e.g. forest ravens), as well as a decline in some arboreal foragers that are dependent on larger patches of intact woodland (e.g. yellow-throated honeyeaters and spotted pardalotes). These findings support the broad concept that the homogenisation of landscape features leads to the homogenisation of biota (Olden & Rooney 2006). Despite great concern over the population trends of birds of prey in Tasmania (Bekessy *et al.* 2009; DPIPWE 2019), and indeed globally (Buechley *et al.* 2019), I found evidence to suggest that numbers of carnivorous birds may be increasing in the Midlands. While my surveys were not designed specifically with the goal of recording raptors, this result does highlight the importance of incorporating farms into survey efforts because processes driving population trends in agricultural landscapes may be unique.

The study of stress in songbirds (Chapter Four) is, to my knowledge, the first study to assess whether conflict with noisy miners might cause physiological stress in other bird species. This is a challenging area of research. Firstly, the window of opportunity for studying small birds that co-occur with miners is narrow, as they are often completely displaced from shared habitats once miner densities exceed a certain threshold (Chapter Three is suggestive of this). Secondly, stress levels are highly context-dependent (Baker *et al.* 2013) and presence of noisy miners is typically confounded by other potential stressors in woodland remnants on farms, making it difficult to distinguish the impacts of competition alone. Nonetheless, I found that superb fairy-wrens living in small woodlands dominated by noisy miners had higher stress (inferred from differential white blood cell counts) than conspecifics living in reserved habitats without miners. Stress levels were highest in fairy-wrens occupying the site with the highest density of noisy miners. I also found a high prevalence of a cosmopolitan genus of avian blood parasite, *Haemoproteus* spp., especially among birds living in reserves. Stress levels were positively related to the presence of *Haemoproteus* and negatively associated with residual mass of fairy-wrens. This subject deserves further attention and I have suggested some promising avenues of investigation.

My study of predation on nests and breeding success (Chapter Five) used new technologies to answer an old question, namely whether the rate of nest predation is higher in agricultural areas and thus could be part of the cause of population decline in birds on farms. I found that rates of nest predation in superb fairy-wrens and brown thornbills in the Midlands were no different to those previously recorded for these species in non-agricultural regions and yet the results of Chapter Three suggest that the average density of fairy-wrens at historical survey sites (n = 33) has declined by 27% and densities of brown thornbills by 25%. Contrary to expectations, daily survival of nests was higher at nesting

sites with less dense vegetation and in small woodland remnants where there was more edge habitat. These findings counter those of many earlier studies of nest predation, principally those in Europe and North America where edge effects are expected to negatively impact reproductive success (Paton 1994; Chalfoun *et al.* 2002). This could indicate a fundamental difference between the nest predator assemblages of temperate Australia and those of other continents.

Australian nest predators appear to be mostly native species of woodland-dependent birds rather than generalists occupying agricultural lands (Zanette & Jenkins 2000; Fulton & Ford 2001; Debus 2006; Fulton 2006; Guppy 2014, this study). Therefore, it isperhaps unsurprising that nest predation is higher in more intact woodlands. Australian songbirds also tend to have higher levels of natural nest predation, small clutch sizes, longer breeding seasons and higher adult survival (Ford *et al.* 2001). Certainly, species including superb fairy-wrens and brown thornbills have adapted for multiple breeding attempts in a season to compensate for their high risk of nest predation. Ford *et al.* (2001) found no difference in nest success of birds in fragmented and continuous landscapes and suggested that low breeding success of Australian passerines may not be reduced any further by habitat fragmentation. The results of Chapter Five indicate that nest predation may not be an especially significant problem for fairy-wrens and brown thornbills in the Midlands, and perhaps for other songbirds, but restoring structural complexity of midstorey vegetation could nonetheless provide a boost to nest success of these species. This would simultaneously improve foraging opportunities for vulnerable small and medium-sized species (identified in Chapter Three) and provide cover from noisy miners (Chapter Four).

Ain't no miner problem

The influence of noisy miners on other songbirds is a recurring theme of the thesis and is a major conservation challenge throughout eastern Australia. Presence of noisy miners is associated with a lower density of small and medium-sized birds in woodland remnants, is a key driver of bird community composition (Chapter Three) and is potentially a cause of physiological stress in smaller birds (Chapter Four). A study of artificial nest predation in an agricultural region of southern Queensland concluded that noisy miner colonies also disrupt ecological processes important for nest predation. Risk of nest predation appeared to be lower in miner-dominated woodlands despite their being associated with a higher abundance of avian nest predators (Robertson *et al.* 2014). While this is a rather paradoxical result, it is consistent with the findings of Chapter Five. Daily survival rates of fairy-wren and thornbill nests were higher in areas with more edge habitat and at nest sites with lower vegetation density, that is, in habitats also preferred by noisy miners.

It has been suggested that miners might themselves be a nest predator or at least cause damage to eggs of other songbirds through curiosity or aggression (Major *et al.* 1996; Taylor & Ford 1998). I found no evidence that noisy miners interfered with nests. It is possible this was because the nests that I studied were constructed close to the ground. However, it is also possible that some nest abandonment by fairy-wrens living in degraded woodlands was a consequence of nest-building females being chased by noisy miners (observed on at least two occasions).

Other examples of interference competition between native species are rare, especially those where conflict between individuals scales up to have population-level

effects that modify species distributions. In Europe, red foxes (*Vulpes vulpes*) are expanding their range north where they compete with the endangered arctic fox (*Alopex lagopus*). Conflict with red foxes for breeding dens has excluded the smaller arctic fox from lower altitude habitats, where food is more abundant, and could be contributing to their decline (Tannerfeldt *et al.* 2002). Urbanisation in Washington is thought to have increased aggressive interactions between a forest specialist, the Pacific wren (*Troglodytes pacificus*), and a native generalist, Bewick's wren (*Thryomanes bewickii*), resulting in the suppression of Pacific wrens from established urban developments (Farwell & Marzluff 2013). These situations could become more common under the influence of climate change and anthropogenic land use change.

Connecting ornithologists, farmers and restoration practitioners

After arthropods, birds are the taxon most commonly studied to determine the response of animal diversity to ecological restoration (Hale *et al.* 2019). This is mostly because birds are easier to monitor than other vertebrate groups and they tend to occupy restored areas more quickly (Ortega-Alvarez & Lindig-Cisneros 2012). The ecosystem services that birds provide also offer opportunities to use birds as tools for restoring farmland. Indeed, birds are increasingly considered to serve a role in accomplishing habitat restoration through pollination, seed dispersal and nutrient cycling, rather than simply being an outcome of successful restoration (Frick *et al.* 2014; Pesendorfer *et al.* 2016). The potential ecological value of birds to both restoration of natural ecosystems and agricultural productivity could provide common ground on which restoration practitioners and farmers can engage. There is still much to be done in quantifying the economic benefits of birds on

farms (Wenny *et al.* 2011), but with this information, landowners could be more motivated to participate in ecological restoration.

In Chapter Three, I found that small patches of woodland could provide suitable habitat for birds if they were free from the influence of noisy miners. I also recorded many bird species using native grasslands, gorse-dominated areas and paddock trees within pastures to move between woodland remnants and as foraging habitat (e.g. white-fronted chat and tree martin). Chapter Five indicates that, despite the widely-accepted maxim of ecological restoration that bigger is better, breeding success of some birds might actually be greater in small, edge-affected remnants and plantings. Together, these results illustrate that habitat features often considered by restoration practitioners, policy makers and farmers alike to have little conservation value can in fact have important ecological benefits. The view that small landscape features are of little consequence to wildlife is widespread among Australian farmers, meaning that such features are regularly removed because of the view that they are "messy". Yet, in a recent global analysis, Wintle *et al.* (2019) found that small, isolated habitat patches are likely to support disproportionately more unique or rare biodiversity values compared with equivalent sized areas in intact landscapes. Hunter *et al.* (2017) also highlighted that recognition and management of what they called "small natural features" could prove an efficient way of conserving biodiversity. More must be done by researchers to convey that even small investments of land towards conservation, for example by retaining a small patch of woodland or fencing off a paddock tree, can be of high value.

Ornithology is a prolific area of biological research that has been key in developing our understanding of evolution, behaviour and ecology (Mayr 1984). I believe there is much

larger scope for studies of physiology and behaviour in birds to overlap with the biodiversity objectives of restoration ecology. Restoration programs often suffer from a lack of data on local wildlife populations from which biodiversity goals can be set and the progress of restoration gauged (McAlpine *et al.* 2016). Behavioural studies of birds can help inform restoration practitioners which resources are important to local species, provide better metrics of habitat quality than basic presence-absence data and identify how species contribute to ecosystem function (Lindell 2008). Similarly, the integration of physiology and ecological restoration could provide new metrics of restoration success (Cooke & Suski 2008). For instance, stress levels might offer an unambiguous indication of how animals perceive "quality habitat" (Ellis *et al.* 2011). I found in Chapter Four that heterophil-to-lymphocyte ratios and measures of body condition collected from superb fairy-wrens could provide a baseline of physiological stress in birds occupying reference woodlands, against which stress levels of individuals living in restoration sites could be compared. A general hypothesis being that stress in birds occupying restored areas declines as structural attributes of habitat mature. Simple measures like these have the potential to indicate changes in fitness in wild populations that would otherwise be difficult and time-consuming to measure directly. With limited resources (funding, equipment, accessible study sites) it makes sense to incorporate studies that might otherwise lean towards "blue-sky" or theoretical research in ecology and evolution with the conservation-focussed works of restoration ecologists and practitioners.

New techniques: nest cameras and LiDAR

In Chapter Five, I used infrared motion-sensor cameras to monitor nests of two songbird species. This has become a popular method among researchers studying

reproductive success (Cox *et al.* 2012; Guppy 2014; Guppy *et al.* 2017; Ellis *et al.* 2018). Reservations over whether cameras at nesting sites might positively bias estimates of nest predation through attracting the attention of predators appear to be unfounded (Thompson & Burhans 2003; Guppy 2014; Ellis *et al.* 2018). Rather, some studies have found that, if anything, cameras reduce nest predation, perhaps due to neophobic responses in predators (Richardson *et al.* 2009).

The advantages of using cameras to monitor nests in combination with, or in lieu of, traditional nest checks by researchers are three-fold. First, the species responsible for nest predation are usually identified and so causes of nest failure can be better understood (Thompson & Burhans 2003). Second, cameras can reduce the frequency with which researchers need to visit nests and check their contents, minimising risks of nest abandonment, attracting predators to, or otherwise repelling predators from nests (for example through scent trails, Ibanez-Alamo *et al.* 2012). This might also permit researchers to invest greater effort towards achieving larger sample sizes. Third, cameras can provide information regarding parental activity (provisioning or incubation behaviour) near the nest at the time of its failure.

I found that, while cameras were useful, they should not be considered infallible. Some cameras failed to trigger on predation events. This could have resulted from improper camera placement or small predators such as rodents being capable of raiding nests without entering motion detection zones in the camera's range (Reconyx Inc. 2017). Given that cameras were sometimes too slow to trigger on fairy-wrens and thornbills when they attended the nest, it is also possible that predators moved too quickly to be photographed as they approached and exited. Robertson *et al.* (2014) used artificial nests to investigate

nest predation in fragmented woodlands of Queensland and found that 23 predation events attributed to birds based on indentations of plasticine eggs went unrecorded by cameras. Video monitoring might be more appropriate when studying smaller bird species, although this requires a much greater investment of time to analyse footage and may be limited by the battery life of cameras. In addition, cameras may be better suited to studying nest predation in open-cup nesting species rather than dome-shaped nesters. Cameras monitoring fairy-wren and brown thornbill nests were repeatedly triggered by low vegetation that moved in the wind, filling their memory cards. Over the duration of the nesting period, grass and ferns also grew around cameras obstructing their view.

I used terrestrial light detecting and ranging (LiDAR) data in Chapter Five to create three-dimensional models of vegetation structure at nesting sites. This technology has advantages over current methods of quantifying nest concealment and vegetation structure at nesting sites. The data produced by LiDAR are objective and the method of data collection is easily repeated. Using this method, it would be possible to compile a database of nest site data from a range of bird species living in different habitat types. This could allow an interesting analysis of the relationships between habitat structure and nesting success across different species and environments. The main limitation of applying LiDAR methods in ecology is the financial cost, which is currently prohibitive for many researchers. The utility of LiDAR data collected at nest sites could also be improved through the development of more meaningful metrics of habitat structure by remote-sensing specialists. For example, analyses in Chapter Five used the density of LiDAR cloud points as a simple proxy for measurements of vegetation density, but inferences made from LiDAR data could be advanced by accounting for the spatial clustering of cloud points at a scale that is relevant to wildlife.

LiDAR data will be increasingly used in ornithology to predict habitat suitability for birds. Bradbury *et al.* (2005) used airborne LiDAR to measure the height of agricultural crops and predict the distribution of breeding skylarks (*Alauda arvensis*) on farms in the United Kingdom. They also used LiDAR to measure canopy height and structural attributes of woodlands to predict breeding performance of two woodland bird species, great tits (*Parus major*) and blue tits (*Parus caeruleus*). Olsson and Rogers (2009) developed a habitat-use model from LiDAR data to identify priority areas for habitat restoration and the reintroduction of the white stork (*Ciconia ciconia*) in Sweden. Ground-based LiDAR data that capture the structure of low vegetation could also be used in combination with behavioural data collected from animals to model "fearscapes" of species (Olsoy *et al.* 2014). In Tasmania, Koch and Baker (2011) estimated crown cover and senescence of *Eucalyptus* trees using aerial photographs to assess the availability of tree hollows suitable for breeding wildlife. Possibly, LiDAR methods could achieve similar results over broader geographical areas in future. The applications of LiDAR to understanding land use change effects on birds and other wildlife are promising, but it is clear that the full potential of LiDAR is yet to be realised in ecology.

Future directions & innovation in restoration

I strongly encourage a long-term monitoring effort of birdlife at restoration sites such that their effectiveness at providing habitat for birds can be examined over time and early intervention can be made in response to unwanted changes, such as establishment of noisy miners. Survey data collected in Chapter Three will help to provide a baseline from which quantitative goals for restoration can be developed (densities of target species) and will give context to the temporal colonisation of restored areas by birds. Future research could repeat the analyses performed in Chapter Three to track the trajectory of bird

communities at restoration sites as they mature and assess how they compare to those of reference woodlands (Fig. 6.1).

Figure 6.1. Assuming that planting sites might initially support a depauperate bird community dominated by small-bodied and exotic species, comparable to small planting sites surveyed in Chapter Three (Fig. 3.3), there are four pathways that community composition might take as plantings mature. A) community composition may be unchanged despite the growth of vegetation. B) the bird community becomes more diverse, with more specialist species typical of larger and more intact woodlands. C) the bird community initially becomes more diverse, but as trees grow taller and midstorey vegetation density is reduced, noisy miners invade leading to a decline in species richness. D) noisy miners establish at planting sites early on such that only a few large open-country bird species typical of miner-dominated remnant woodlands are able to colonise.

It is important that monitoring of birds occupying restored habitat moves beyond solely measuring occurrence and towards measuring species demography (e.g. survival, age structure and reproductive success) to ensure that "ecological traps" are avoided (Marzluff & Ewing 2001; Belder *et al.* 2018). Restoration sites could constitute ecological traps if animals are attracted to newly established habitat but have reduced fitness relative to individuals living in reference sites (Hale *et al.* 2017). Ecological traps can reduce population persistence and increase the risk of localised extinctions (Hale *et al.* 2015). For small dome-nesting passerines at least, it appears that planting sites will provide suitable nesting habitat because daily survival rates of nests are positively related to the amount of edge habitat and smaller patches of woodland, including planting sites, are likely to support fewer nest predators. It is unknown, however, just how much of a threat feral cats might pose to adult birds living in revegetated corridors, given their preference to use edges of vegetation patches and linear habitats (Doherty *et al.* 2014).

The business of ecological restoration is typically risk-averse due to the inherent uncertainties involved in working with natural processes. Restoration practitioners are, as a consequence, frequently unwilling to innovate for fear of restoration programs failing and the ever-present need to be cost-effective (Mohr & Metcalf 2018). This must change if conservation outcomes of ecological restoration are to improve. In Chapter Three, I suggest trialling new configurations of plantings to test for the most noisy miner-resilient, including the use of dense, exotic plant species. I also identified that spiny invasive weeds such as gorse are good quality nesting habitat and provide birds in the Midlands with protection from predators. Gorse can be useful to a range of native animals, at least until native vegetation that offers similar function is established (Ranyard *et al.* 2018). Artificial structures might also be trialled for their effectiveness in promoting the succession of

farmland in the Midlands. Restoration managers of forests in the Northern Hemisphere and tropical regions have fostered the return of birds to degraded lands by installing perching structures, with the ultimate goal of increasing levels of seed rain (Mcclanahan & Wolfe 1993; Holl *et al.* 2000). Seed rain, seed establishment and species richness of seed rain is greater under artificial perches than in open control environments (Guidetti *et al.* 2016). Yet, in their meta-analysis, Guidetti *et al.* (2016) found no studies that measured how effective perches are in ecological restoration in Oceania. In temperate woodlands of Australia, fleshy-fruited plants that rely on animal-mediated dispersal are less common, fruit is available only on a seasonal basis, and frugivorous birds are comparatively rare (Stanley & Lill 2002). Nonetheless, perches and feeding stations might help to encourage birds' dispersal of native seeds and fruits, for example, from the spiky treeviolet (a species identified as a suitable nesting plant in Chapter Five, *Hymenanthera dentata*) or the hemiparasitic native cherry (*Exocarpos cupressiformis*), which anecdotally, germinates more successfully after ingestion by birds and is difficult to establish in plantings. It is important in this agricultural setting, though, that bird-mediated dispersal of weeds including hawthorn (*Crataegus monogyna*) and blackberry (*Rubus* spp.) and the invasion of productive farmland by native plants is avoided in order to maintain good relationships with landowners.

My results offer support for the conservation value of a more novel restored landscape. This is especially because the Midlands has been degraded for so long that a clearly-defined historical state is, in some parts, unknown. Deliberate creation of novel ecosystems can be controversial because of the perception that this "lowers the bar" for restoration ecology, and could be risky if our understanding and ability to manage ecosystems is overestimated (Perring *et al.* 2013). Novel ecosystems may, however, be a

necessary bridge to cross until more appropriate solutions to the threats facing wildlife are identified.

Conclusion

Declines in farmland biodiversity are ongoing and may worsen under current trends of agricultural intensification. This threatens not only wildlife populations but also agricultural productivity in the long-term. Ecological restoration will play a critical role in the recovery of native wildlife and the maintenance of ecosystem services on farms. The thesis identified elements of habitat that are most important for the persistence of woodland birds in agricultural landscapes of Tasmania. My results suggest there are several pathways and end points that are possible for ecological restoration in the Midlands. Future research should examine ways in which we can increase the likelihood that revegetation and restored woodlands move towards supporting diverse and resilient bird communities, and test interventions that improve that. Better integration of restoration ecology with behavioural and physiological studies of birds will improve our understanding of how they perceive habitat quality, the mechanisms causing avian decline and our ability to address these through habitat restoration.

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Appendices

Sunset over native grassland at "Beaufront".

Appendix A

Appendix A.1 List of bird species recorded during transect surveys.

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Australian Hobby	***Falco longipennis***	*LC*	Vertebrates	R	Nat.Tas	L	Aer
Southern Australian Hobby	*Falco longipennis longipennis*	*LC*					
Australian Magpie	***Gymnorhina tibicen***	*LC*	Invertebrates	R	Nat.Tas	L	Ter
Tasmanian Australian Magpie	*Gymnorhina tibicen hypoleuca*	*LC*					
Australian Shelduck	***Tadorna tadornoides***	*LC*	Invertebrates, Plants	N	Nat.Tas	VL	AqTer
Australian Wood Duck	***Chenonetta jubata***	*LC*	Invertebrates, Plants	N	Nat.Tas	L	AqTer
Beautiful Firetail	***Stagonopleura bella***	*LC*	Seeds	R	Nat.Tas	S	Ter
South-eastern Beautiful Firetail	*Stagonopleura bella bella*	*LC*					
Black Currawong	***Strepera fuliginosa***	*LC*	Invertebrates, Vertebrates	N	End.Tas	L	Ter
Tasmanian Black Currawong	*Strepera fuliginosa fuliginosa*	*LC*					
Black-faced Cuckoo-shrike	***Coracina novaehollandiae***	*LC*	Invertebrates	M	Nat.Tas	L	Arb
Tasmanian Black-faced Cuckoo-shrike	*Coracina novaehollandiae novaehollandiae*	*LC*					
Black-headed Honeyeater	***Melithreptus affinis***	*LC*	Invertebrates	R	End.Tas	S	Arb

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Blue-winged Parrot	***Neophema chrysostoma***	*LC*	Seeds	M	Nat.Tas	M	Ter
Brown Falcon	***Falco berigora***	*LC*	Vertebrates	R*	Nat.Tas	L	Aer
Australian Brown Falcon	*Falco berigora berigora*	*LC*					
Brown Goshawk	***Accipiter fasciatus***	*LC*	Vertebrates	R*	Nat.Tas	L	Aer
Southern Brown Goshawk	*Accipiter fasciatus fasciatus*	*LC*					
Brown Quail	***Synoicus ypsilophorus***	*LC*	Invertebrates, Seeds	R	Nat.Tas	L	Ter
Tasmanian Brown Quail	*Synoicus ypsilophorus ypsilophorus*	*LC*					
Brown Thornbill	***Acanthiza pusilla***	*LC*	Invertebrates	R	Nat.Tas	S	Arb
Tasmanian Brown Thornbill	*Acanthiza pusilla diemenensis*	*LC*					
Brush Bronzewing	***Phaps elegans***	*LC*	Seeds	R	Nat.Tas	L	Ter
Eastern Brush Bronzewing	*Phaps elegans elegans*	*LC*					
Chestnut Teal	***Anas castanea***	*LC*	Invertebrates, Plants	N	Nat.Tas	L	Aqu
Collared Sparrowhawk	***Accipiter cirrocephalus***	*LC*	Vertebrates	N	Nat.Tas	L	Aer
Australian Collared Sparrowhawk	*Accipiter cirrocephalus cirrhocephalis*	*LC*					
Common Blackbird	***Turdus merula***	*I*	Invertebrates	R	Exo.Aus	M	Ter
Common Bronzewing	***Phaps chalcoptera***	*LC*	Seeds	R	Nat.Tas	L	Ter
Common Pheasant	***Phasianus colchicus***	*I*	Invertebrates, Plants	R	Exo.Aus	VL	Ter
Common Starling	***Sturnus vulgaris***	*I*	Invertebrates	R	Exo.Aus	M	Ter

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Crescent Honeyeater	***Phylidonyris pyrrhopterus***	*LC*	Nectar	N	Nat.Tas	S	Arb
Eastern Crescent Honeyeater	*Phylidonyris pyrrhopterus pyrrhopterus*	*LC*					
Dusky Robin	***Melanodryas vittata***	*LC*	Invertebrates	R	End.Tas	M	Ter
Tasmanian Dusky Robin	*Melanodryas vittata vittata*	*LC*					
Dusky Woodswallow	***Artamus cyanopterus***	*LC*	Invertebrates	M	Nat.Tas	M	Aer
Eastern Dusky Woodswallow	*Artamus cyanopterus cyanopterus*	*LC*					
Eastern Rosella	***Platycercus eximius***	*LC*	Seeds	R	Nat.Tas	M	Ter
Tasmanian Eastern Rosella	*Platycercus eximius diemenensis*	*LC*					
Eastern Spinebill	***Acanthorhynchus tenuirostris***	*LC*	Nectar	N	Nat.Tas	S	Arb
Tasmanian Eastern Spinebill	*Acanthorhynchus tenuirostris dubius*	*LC*					
European Goldfinch	***Carduelis carduelis***	*I*	Seeds	R	Exo.Aus	S	Ter
Fan-tailed Cuckoo	***Cacomantis flabelliformis***	*LC*	Invertebrates	M	Nat.Tas	M	Arb
Australian Fan-tailed Cuckoo	*Cacomantis flabelliformis flabelliformis*	*LC*					
Flame Robin	***Petroica phoenicea***	*NT*	Invertebrates	M	Nat.Tas	S	Ter
Forest Raven	***Corvus tasmanicus***	*LC*	Invertebrates , Vertebrates	R	Nat.Tas	L	ArTer
Southern Forest Raven	*Corvus tasmanicus tasmanicus*	*LC*					

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Galah	***Eolophus roseicapilla***	*LC*	Seeds	R	Nat.Tas *	L	Ter
Eastern Galah	*Eolophus roseicapilla albiceps*	*LC*					
Golden Whistler	***Pachycephala pectoralis***	*LC*	Invertebrates	R	Nat.Tas	M	Arb
Tasmanian Golden Whistler	*Pachycephala pectoralis glaucura*	*LC*					
Common Greenfinch	***Chloris chloris***	*I*	Seeds	R	Exo.Aus	M	Ter
Green Rosella	***Platycercus caledonicus***	*LC*	Seeds	R	End.Tas	L	Arb
Tasmanian Green Rosella	*Platycercus caledonicus caledonicus*	*LC*					
Grey Butcherbird	***Cracticus torquatus***	*LC*	Invertebrates , Vertebrates	R	Nat.Tas	M	ArTer
Tasmanian Grey Butcherbird	*Cracticus torquatus cinereus*	*LC*					
Grey Currawong	***Strepera versicolor***	*LC*	Invertebrates , Vertebrates	R	Nat.Tas	L	ArTer
Tasmanian Grey Currawong	*Strepera versicolor arguta*	*LC*					
Grey Fantail	***Rhipidura fuliginosa***	*LC*	Invertebrates	N	Nat.Tas	S	Arb
Tasmanian Grey Fantail	*Rhipidura fuliginosa albiscapa*	*LC*					
Grey Goshawk	***Accipiter novaehollandiae***	*LC*	Vertebrates	R	Nat.Tas	L	Aer
Grey Shrike-thrush	***Colluricincla harmonica***	*LC*	Invertebrates , Vertebrates	R	Nat.Tas	M	ArTer
Tasmanian Grey Shrike-thrush	*Colluricincla harmonica strigata*	*LC*					

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
House Sparrow	***Passer domesticus***	*I*	Invertebrates, Seeds	R	Exo.Aus	M	Ter
Laughing Kookaburra	***Dacelo novaeguineae***	*LC*	Invertebrates, Vertebrates	R	Exo.Tas	L	Arb
Southern Laughing Kookaburra	*Dacelo novaeguineae novaeguineae*	*LC*					
Little Wattlebird	***Anthochaera chrysoptera***	*LC*	Nectar	N	Nat.Tas	M	Arb
Tasmanian Little Wattlebird	*Anthochaera chrysoptera tasmanica*	*LC*					
Little Corella	***Cacatua sanguinea***	*LC*	Seeds	R	Exo.Tas	L	Ter
Eastern Little Corella	*Cacatua sanguinea gymnopis*	*LC*					
Long-billed Corella	***Cacatua tenuirostris***	*LC*	Seeds	R	Exo.Tas	L	Ter
Musk Lorikeet	***Glossopsitta concinna***	*LC*	Nectar	N	Nat.Tas	M	Arb
Tasmanian Musk Lorikeet	*Glossopsitta concinna didimus*	*LC*					
Nankeen Kestrel	***Falco cenchroides***	*LC*	Vertebrates	M	Nat.Tas	L	Aer
Australasian Nankeen Kestrel	*Falco cenchroides cenchroides*	*LC*					
New Holland Honeyeater	***Phylidonyris novaehollandiae***	*LC*	Nectar	R	Nat.Tas	S	Arb
Tasmanian New Holland Honeyeater	*Phylidonyris novaehollandiae canescens*	*LC*					
Noisy Miner	***Manorina melanocephala***	*LC*	Invertebrates	R	Nat.Tas	M	Arb
Tasmanian Noisy Miner	*Manorina melanocephala leachi*	*LC*					

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Olive Whistler	***Pachycephala olivacea***	*LC*	Invertebrates	R	Nat.Tas	M	Arb
Tasmanian Olive Whistler	*Pachycephala olivacea apatetes*	*LC*					
Pacific Black Duck	***Anas superciliosa***	*LC*	Invertebrates , Plants	N	Nat.Tas	VL	Aqu
Pallid Cuckoo	***Heteroscenes pallidus***	*LC*	Invertebrates	M	Nat.Tas	M	Arb
Pink Robin	***Petroica rodinogaster***	*LC*	Invertebrates	R	Nat.Tas	S	Ter
Tasmanian Pink Robin	*Petroica rodinogaster rodinogaster*	*LC*					
Satin Flycatcher	***Myiagra cyanoleuca***	*LC*	Invertebrates	M	Nat.Tas	S	Arb
Scarlet Robin	***Petroica multicolor***	*LC*	Invertebrates	R	Nat.Tas	S	Ter
Tasmanian Scarlet Robin	*Petroica multicolor leggii*	*LC*					
Shining Bronze-Cuckoo	***Chalcites lucidus***	*LC*	Invertebrates	M	Nat.Tas	M	Arb
Australian Shining Bronze-Cuckoo	*Chalcites lucidus plagosus*	*LC*					
Silvereye	***Zosterops lateralis***	*LC*	Invertebrates	M	Nat.Tas	S	Arb
Tasmanian Silvereye	*Zosterops lateralis lateralis*	*LC*					
Spotted Pardalote	***Pardalotus punctatus***	*LC*	Invertebrates	R	Nat.Tas	S	Arb
Coastal Spotted Pardalote	*Pardalotus punctatus punctatus*	*LC*					
Striated Pardalote	***Pardalotus striatus***	*LC*	Invertebrates	M	Nat.Tas	S	Arb
Tasmanian Striated Pardalote	*Pardalotus striatus striatus*	*LC*					
Strong-billed Honeyeater	***Melithreptus validirostris***	*LC*	Invertebrates	R	End.Tas	M	Arb
Sulphur-crested Cockatoo	***Cacatua galerita***	*LC*	Seeds	R	Nat.Tas	L	Ter

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Eastern Sulphur-crested Cockatoo	*Cacatua galerita galerita*	*LC*					
Superb Fairy-wren	***Malurus cyaneus***	*LC*	Invertebrates	R	Nat.Tas	S	Ter
Tasmanian Superb Fairy-wren	*Malurus cyaneus cyaneus*	*LC*					
Swamp Harrier	***Circus approximans***	*LC*	Vertebrates	M	Nat.Tas	L	Aer
Tasmanian Scrubwren	***Sericornis humilis***	*LC*	Invertebrates	R	End.Tas	S	Ter
Southern Tasmanian Scrubwren	*Sericornis humilis humilis*	*LC*					
Tree Martin	***Petrochelidon nigricans***	*LC*	Invertebrates	M	Nat.Tas	S	Aer
Tasmanian Tree Martin	*Petrochelidon nigricans nigricans*	*LC*					
Wedge-tailed Eagle	***Aquila audax***	*LC*	Vertebrates	R	Nat.Tas	VL	Aer
Tasmanian Wedge-tailed Eagle	*Aquila audax fleayi*	*V*					
Welcome Swallow	***Hirundo neoxena***	*LC*	Invertebrates	M	Nat.Tas	S	Aer
Eastern Welcome Swallow	*Hirundo neoxena neoxena*	*LC*					
White-faced Heron	***Egretta novaehollandiae***	*LC*	Vertebrates	N	Nat.Tas	L	Aqu
White-fronted Chat	***Epthianura albifrons***	*LC*	Invertebrates	N	Nat.Tas	S	Ter
Yellow Wattlebird	***Anthochaera paradoxa***	*LC*	Nectar	N*	End.Tas	L	Arb
Tasmanian Yellow Wattlebird	*Anthochaera paradoxa paradoxa*	*LC*					
Yellow-rumped Thornbill	***Acanthiza chrysorrhoa***	*LC*	Invertebrates	R*	Nat.Tas	S	Ter
Tasmanian Yellow-rumped Thornbill	*Acanthiza chrysorrhoa leachi*	*LC*					
Yellow-tailed Black-Cockatoo	***Zanda funereus***	*LC*	Seeds	N	Nat.Tas	L	Arb

Tasmanian Yellow-tailed Black-Cockatoo	*Zanda funereus xanthanota*	*LC*					
Yellow-throated Honeyeater	***Nesoptilotis flavicollis***	*LC*	Invertebrates	R	End.Tas	M	Arb

[a] Species level names are in bold and the relevant subspecies is listed below. All names are derived from the Working List of Australian Birds Version 2.1.

[b] Australian conservation status is derived from the Working List of Australian Birds. LC = least concern, V = vulnerable, NT = near threatened, EN = endangered, CE = critically endangered, I = introduced

[c] Diet information is derived from the Handbook of Australian, New Zealand and Antarctic Birds.

[d] Movement information is derived from the Handbook of Australian, New Zealand and Antarctic Birds. Asterisk denotes that knowledge of migration is unknown, unclear or varies by geographic region.

[e] Nat.Tas = native to Tasmania, End.Tas = endemic Tasmanian species, Exo.Tas = exotic to Tasmania from the Australian mainland, Exo.Aus = exotic to Australia including Tasmania. Conflicting information exists on whether galahs are native to Tasmania or not.

[f] Body size was classified as described in Chapter Three. S = small, M = medium, L = large, VL = very large.

[g] Arb = arboreal, Aer = aerial forager, Aqu = aquatic forager, Ter = terrestrial / ground forager, ArTer = species that forage both arboreally and on the ground, AqTer = species that forage both on water and on the ground.

Appendix A.1 List of species recorded only during 2 ha / 20 minute surveys of woodland or planting sites.

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Tawny Frogmouth	***Podargus strigoides***	*LC*	Invertebrates , Vertebrates	R	Nat.Tas	L	Arb
Eastern Tawny Frogmouth	*Podargus strigoides strigoides*	*LC*					
Silver Gull	***Chroicocephalus novaehollandiae***	*LC*	Invertebrates , Vertebrates	N	Nat.Tas	L	Aqu
Australian Silver Gull	*Chroicocephalus novaehollandiae novaehollandiae*	*LC*					
White-bellied Sea-Eagle	***Haliaeetus leucogaster***	*LC*	Vertebrates	R	Nat.Tas	VL	Aer
Tasmanian Native-hen	***Tribonyx mortierii***	*LC*	Plants	R	End.Tas	VL	Ter
Peregrine Falcon	***Falco peregrinus***	*LC*	Vertebrates	R	Nat.Tas	L	Aer
Australian Peregrine Falcon	*Falco peregrinus macropus*	*LC*					
Masked Lapwing	***Vanellus miles***	*LC*	Invertebrates	R	Nat.Tas	L	Ter
Southern Masked Lapwing	*Vanellus miles novaehollandiae*	*LC*					
Grey Teal	***Anas gracilis***	*LC*	Invertebrates , Plants	N	Nat.Tas	L	Aqu
Great Cormorant	***Phalacrocorax carbo***	*LC*	Vertebrates	N	Nat.Tas	VL	Aqu
Australian Great Cormorant	*Phalacrocorax carbo carboides*	*LC*					

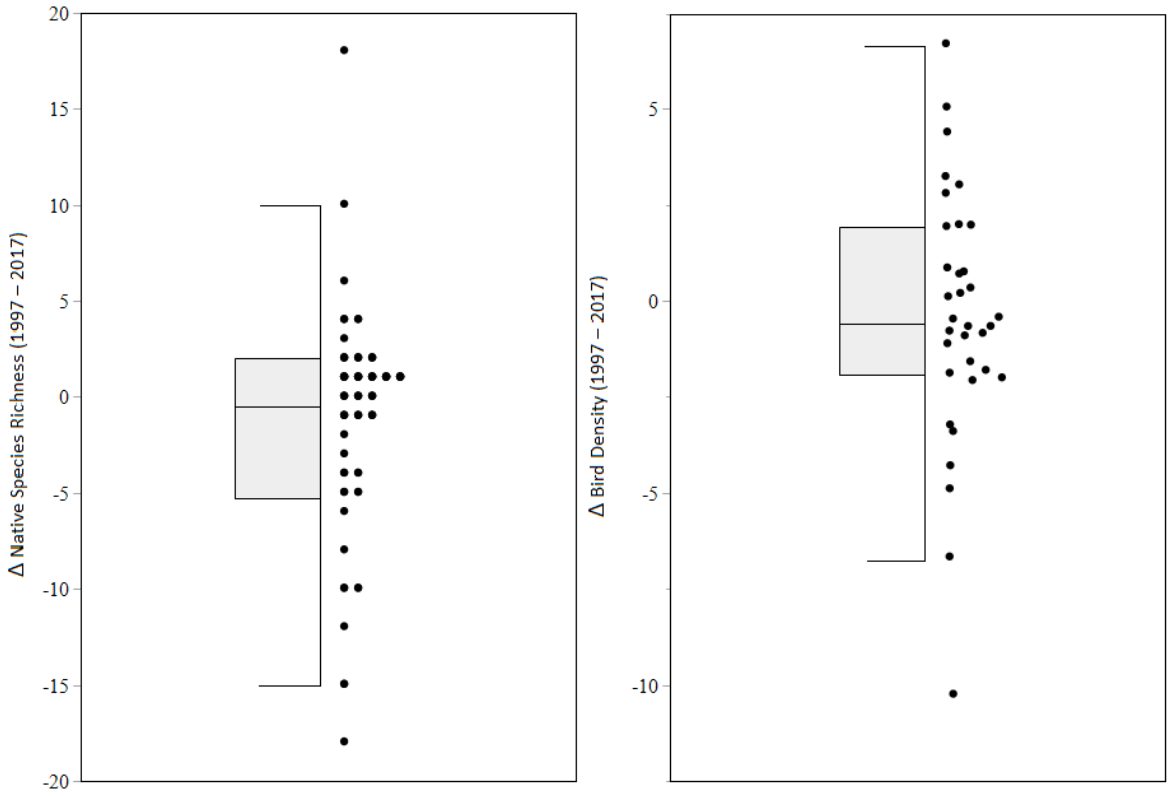
Appendix A.1 List of species recorded only during 2 ha / 20 minute surveys of native grasslands or pasture sites.

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Striated Fieldwren	***Calamanthus fuliginosus***	*LC*	Invertebrates	R	Nat.Tas	S	Ter
Eastern Tasmanian Striated Fieldwren	*Calamanthus fuliginosus fuliginosus*	*LC*					
Eurasian Skylark	***Alauda arvensis***	*I*	Invertebrates, Seeds	R	Exo.Aus	M	Ter
Banded Lapwing	***Vanellus tricolor***	*LC*	Invertebrates, Plants	N	Nat.Tas	L	Ter
Australasian Pipit	***Anthus novaeseelandiae***	*LC*	Invertebrates, Seeds	N	Nat.Tas	M	Ter
Tasmanian Australian Pipit	*Anthus novaeseelandiae bistriatus*	*LC*					

Appendix A.1 List of species heard offsite during surveys or that were recorded incidentally.

Common Name[a]	Scientific Name	Conservation Status[b]	Diet[c]	Movement[d]	Native Status[e]	Body Size[f]	Foraging Height[g]
Turkey	***Meleagris***	*I*	Plants	R	Exo.Aus	VL	Ter
Swift Parrot	***Lathamus discolor***	*CE*	Nectar	M	Nat.Tas	M	Arb
Spotted Dove	***Streptopelia chinensis***	*I*	Seeds	R	Exo.Aus	L	Ter
Red Junglefowl	***Gallus gallus***	*I*	Invertebrates, Plants	R	Exo.Aus	L	Ter
Indian Peafowl	***Pavo cristatus***	*I*	Invertebrates, Plants	R	Exo.Aus	VL	Ter
Helmeted Guineafowl	***Numida meleagris***	*I*	Invertebrates, Seeds	R	Exo.Aus	VL	Ter
Horsfield's Bronze-Cuckoo	***Chalcites basalis***	*LC*	Invertebrates	M	Nat.Tas	S	Ter
Black Swan	***Cygnus atratus***	*LC*	Plants	R	Nat.Tas	VL	Aqu
Masked Owl	***Tyto novaehollandiae***	*LC*	Vertebrates	R	Nat.Tas	VL	Aer
Tasmanian Masked Owl	*Tyto novaehollandiae castanops*	*EN*					
Tasmanian Boobook	***Ninox leucopsis***	*LC*	Vertebrates	M*	Nat.Tas	L	Aer
Tasmanian Thornbill	***Acanthiza ewingii***	*LC*	Invertebrates	R	End.Tas	S	Arb
Southern Tasmanian Thornbill	*Acanthiza ewingii ewingii*	*LC*					

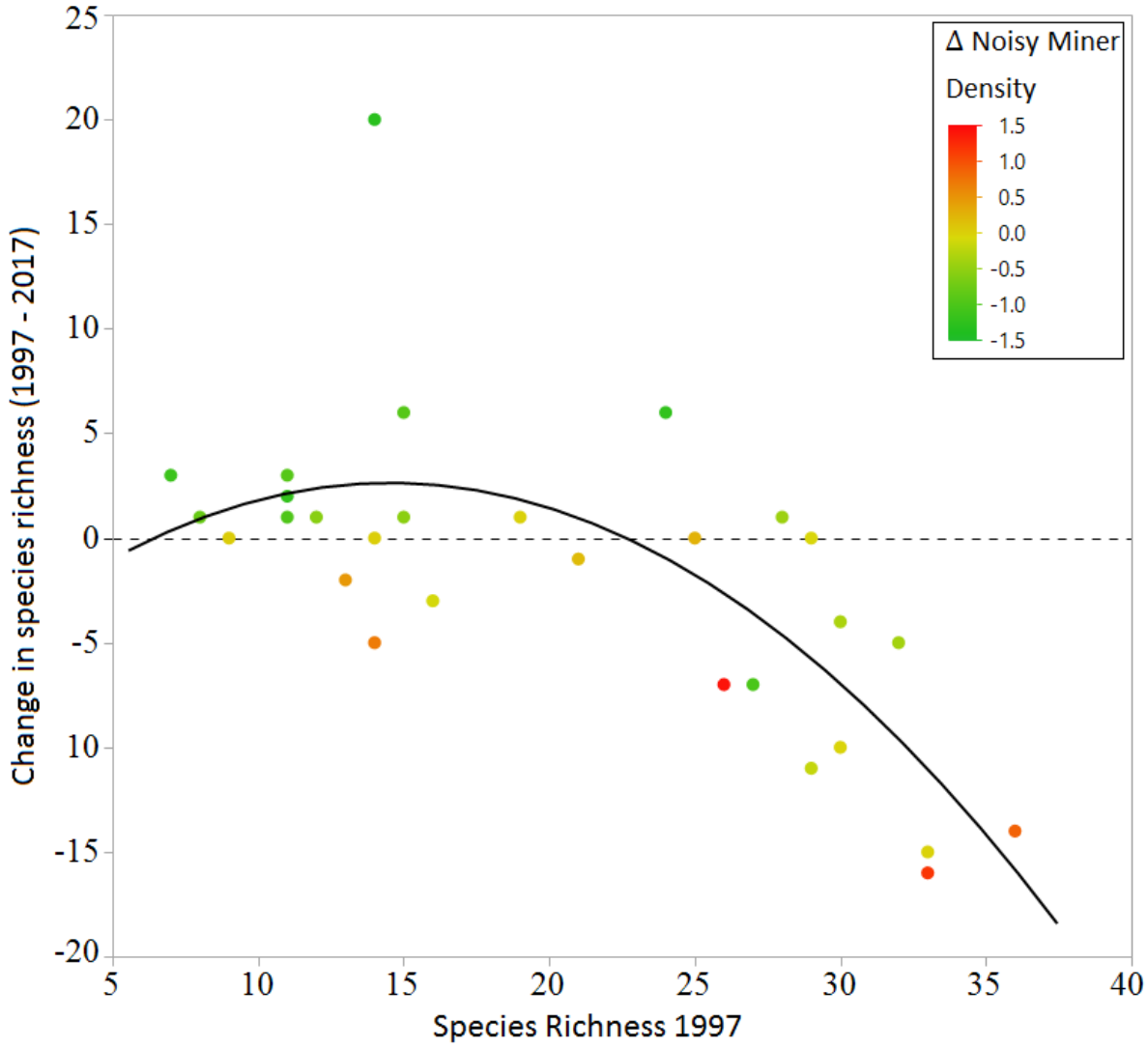
Appendix A.2 Change in native species richness and bird density (birds hectare^{-1}) at historical survey sites between the 1997 and 2017 survey periods.



Appendix A.3 Models with weight < 0.10 of the relationship between change in species richness at historical survey sites and changes in noisy miner density, woody vegetation cover, patch size, change in patch size and the number of centre pivot irrigators within 1 km.

Δ Native Species Richness							
AIC*c*	Δ AIC*c*	*W*	Δ Noisy Miner Density	Δ Woody Vegetation Cover	Patch Size	Δ Patch Size	Pivot Irrigators
213.18	2.82	0.09	-5.415 ± 1.393	0.387 ± 0.184	0.004 ± 0.002	-	0.261 ± 0.648
215.08	4.72	0.04	-5.819 ± 1.440	0.435 ± 0.189	0.004 ± 0.002	0.251 ± 0.237	0.289 ± 0.647
221.24	10.88	0.00	-	0.537 ± 0.217	-	-	-
225.74	15.38	0.00	-	-	0.003 ± 0003	-	-
230.53	20.17	0.00	-	-	0.003 ± 0.003	-0.201 ± 0.293	0.203 ± 0.293

Appendix A.4 Change in native bird species richness at historical survey sites (*n* = 33) plotted against their initial richness in the 1997 survey period. Colour of data points indicates the change in noisy miner density (miners hectare^{-1}) at each site. The dashed line indicates a zero net change in species richness.



Appendix B

Appendix B.1 Results of spring models of Heterophil : Lymphocyte ratio (log_{10}-transformed H:L) in superb fairy-wrens that had model weights > 0.10 and winter models of H:L ratio.

Spring Models								
AIC*c*	Δ AIC*c*	*W*	R^2 (Adj.R^2)	Fragment Type	Parasite Prevalence	Fragment Type × Parasite Pres.	Sex	Time
30.75	3.51	0.08	0.10 (0.09)	0.189 ± 0.069	-	-	-	-
30.83	3.58	0.07	0.16 (0.12)	0.188 ± 0.068	-	-	0.099 ± 0.068	-0.142 ± 0.098
36.59	9.34	0.00	0.23 (0.04)	-	0.111 ± 0.071	-	0.096 ± 0.071	-0.144 ± 0.102
Winter Models								
AIC*c*	Δ AIC*c*	*W*	R^2 (Adj.R^2)	Fragment Type	Parasite Prevalence	Fragment Type × Parasite Pres.	Sex	Time
45.52	0.00	0.64	0.02 (-0.02)	0.150 ± 0.219	-	-	-	-
48.14	2.63	0.17	0.03 (-0.06)	0.175 ± 0.230	0.128 ± 0.285	-	-	-
49.24	3.72	0.10	0.12 (-0.02)	0.227 ± 0.228	-	-	-0.274 ± 0.228	0.139 ± 0.228
50.30	4.78	0.06	0.08 (-0.07)	-	0.082 ± 0.284	-	-0.220 ± 0.226	0.132 ± 0.237
52.28	6.77	0.02	0.14 (-0.05)	0.271 ± 0.242	0.181 ± 0.296	-	-0.307 ± 0.238	0.110 ± 0.236
53.56	8.04	0.01	0.21 (0.00)	0.392 ± 0.250	0.396 ± 0.324	-0.949 ± 0.651	-0.278 ± 0.232	0.144 ± 0.231

Appendix B.2 Results of models of packed cell volume and residual mass in superb fairy-wrens that had weights > 0.10.

Response Variable	AIC*c*	Δ AIC*c*	*W*	Adj.R^2	Fragment Type	Parasite Presence	Sex	Time	Season
Residual mass	234.10	7.20	0.03	0.11	-	0.334 ± 0.171	-	-	-
	235.21	8.32	0.01	0.11	-0.018 ± 0.172	0.380 ± 0.177	-	-	-
PCV	651.12	3.46	0.08	0.03	2.688 ± 1.688	-0.685 ± 1.722	-	-	-
	651.52	3.86	0.06	0.03	-	-0.100 ± 1.664	-	-	-
	653.29	5.63	0.03	0.03	2.494 ± 1.630	-	-0.480 ± 1.634	-0.741 ± 1.891	-

Appendix C

Appendix C.1 A priori candidate models used to examine nest predation in superb fairy-wrens and brown thornbills as a function of temporal and habitat factors. We combined best-fit nest-site models with candidate models at the landscape level scale to produce the final model set. Descriptions of habitat factors are provided in Table 5.1.

Temporal Models	Nest-site Models	Final Model Set
Year	Height	Height
Time	Height + Points 1.5	Height + Edge 100
Null	Height + Points Nest	Height + Points 1.5
	Height + Canopy Closure	Height + Wood 500 + Points 1.5
	Height + Concealment	Height + Wood 100 + Edge 100
	Height + Skew	Height + Edge 50 + Wood 100 + Points 1.5
	Height × Points Nest	Height + Edge 100 + Wood 100 + Points 1.5
	Height × Concealment	Height + Edge 100 + Wood 500 + Points 1.5
	Height + Points 1.5 + Canopy Height	Height × Edge 100
	Height + Points 1.5 + Concealment	Height × Distance Edge
	Points 1.5	Height × Edge 100 + Wood 100
	Points 1.5 + Canopy Height	Height × Edge 50 + Wood 100 + Points 1.5
	Points Nest	Height × Edge 100 + Wood 100 + Points 1.5
	Concealment	Height × Edge 100 + Wood 500 + Points 1.5
	Null	Height × Edge 500 + Wood 500 + Points 1.5
		Height × Distance Edge + Edge 100 + Points 1.5
		Wood 100 + Edge 100
		Wood 500 + Edge 100
		Points 1.5
		Null